Distribution of the invasive seaweed *Undaria pinnatifida* in Lyttelton Harbour, New Zealand, and its interactions with native mussel reef communities

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Abstract

Invasions by non-native species are becoming an increasingly significant issue worldwide in terrestrial, freshwater and marine environments. Invasive species encroach into the habitats of native species and communities, where they can change local community structure and ecosystem functions. However, ecological impacts on invaded ecosystems and specific native species have been documented only for a small fraction of invasive species. One of the most widely distributed marine invaders worldwide is the Japanese kelp *Undaria pinnatifida* ((Harvey) Suringar, 1873). Here I investigated the distribution of *Undaria* in Lyttelton Harbour, New Zealand, its interactions with the native New Zealand habitat-dominating mussel *Perna canaliculus*, and their respective effects on the associated algal and invertebrate community.

Undaria was first recorded in Lyttelton in 1989. In this thesis I documented, through spatial and temporal surveys, that *Undaria* today can be found throughout most of the harbour in the low intertidal zone and that individuals of *Undaria* often are attached to, or interspersed around, mussel aggregations in this low intertidal zone. Although *Undaria* is an annual kelp that typically has a unimodal winter-dominated growth pattern, I also found that its abundance fluctuated less over the year when it co-occurred with mussels. This unexpected phenological pattern is likely caused by less synchronous overlapping generations coupled with a longer growing season, possibly triggered by localized higher wave action, rather than being driven by mussels themselves or individual *Undaria* plants persisting for an entire year.

To investigate potential impacts of *Undaria* on *Perna* and mussel-associated sessile and mobile communities, mussels with and without attached *Undaria* were collected every month for one year. The health of the mussels was measured using the 'condition index', and the algae and invertebrates associated with the mussel were recorded. I found that the condition index of *Perna* significantly decreased when an *Undaria* individual was attached. However, there were no (or very weak) effects of *Undaria* on algae and sessile invertebrates attached to mussels, although mobile invertebrate communities were significantly more species-rich and abundant in the presence of *Undaria*. This suggests that *Undaria* provides a

new habitat for many mobile invertebrates, particularly crustaceans and gastropods, where they are likely to experience more food and less desiccation, wave stress and predation.

Finally, I tested experimentally for effects of (a) *Perna* on *Undaria* recruitment, (b) *Undaria* on *Perna* recruitment and (c) of both species on associated algal and invertebrate communities, through a factorial removal experiment. Both *Undaria* and *Perna* were removed monthly over a period of one year from 0.25 x 0.25 m plots and algae and mobile and sessile invertebrates were quantified after 10, 15 and 25 months. I found that more *Undaria* recruited into plots with *Perna* than without. Community composition was only slightly affected by *Undaria* presence, whereas *Perna* had a more marked effect, especially on the invertebrate community and on canopy-forming algal species. Furthermore, an unprecedented hot summer in 2017/18 appeared to reduce the cover of most species in the plots at the final sampling date, after which *Undaria* colonized plots where native algal species had dominated prior to the hot summer.

Invasive species continue to expand their ranges as a result of globalised trade and modern shipping and transport systems. Even though *Undaria* appears to have had only limited effects on the reef community, this study reported negative impacts of *Undaria* on *Perna*, a very important native habitat-former and aquacultural product, and that *Perna*, like other native species, can facilitate invasion of non-native species. Further experimental research is required to determine the exact underpinning mechanisms that cause these interactions. Nevertheless, my study highlights a topic that has not been investigated in detail. My findings may also have implications for marine aquaculture, particularly mussel-culturing, were, for example, *Undaria* removals could improve mussel condition and thereby provide a better product.

1 General introduction

1.1 Biological invasions and invasive seaweeds

As global trade has increased and trade networks have become more connected, there has been an increasing number of species becoming unintentionally transported outside of their natural ranges, including in the marine environment (Hulme 2009, Keller et al. 2011). While not all of introduced species become established outside their native range, some become successful invaders, including numerous algal and invertebrate species (Williams and Smith 2007, Galil 2009, Thomsen et al. 2016a). These invasive species have the potential to cause significant ecological impact by out-competing native species and otherwise changing ecological relationships (Clavero and Garcia-Berthou 2005, Didham et al. 2005, Molnar et al. 2008, Thomsen et al. 2009, Katsanevakis et al. 2014). Invasive species can create economic losses as they interfere with agricultural and aquaculture systems and decrease export value (Pimentel et al. 2005, Kluza et al. 2006, Howes et al. 2007). Approximately 20% of the 100 worst invasive species in the world are aquatic fish, invertebrates and plants (Lowe et al. 2000).

Many governments across the world have established lists of marine pests and potential marine invaders based on species invasion history and likelihood of arrivals and establishment (Molnar et al. 2008, Champion et al. 2014). In addition, pre- and post-invasion biosecurity strategies have been developed to deal with the issue (Williams and West 2000, Wotton et al. 2004). However, knowledge of the exact effects of marine invasive species remains unclear, and the full ecological implications are typically unknown (Lourey et al. 2000, Ross et al. 2004). More specifically, key questions remain about the implications for the wider ecosystem, cascades, predator-prey interactions, and specific relationships between particular species.

Due to the connected nature of open marine systems (Carr et al. 2003), it is difficult to contain and control newly introduced species. There have been very few recorded instances of unwanted species that were successfully removed from a marine setting (Culver and Kuris 2000). Many marine species have microscopic juvenile life stages and broadcast spawning behaviour which means they are able to spread quickly once they have been introduced.

Algal marine invaders can cause dramatic shifts in ecosystem composition as they can potentially out-compete and replace native seaweed species (Schaffelke et al. 2006, Thomsen et al. 2009, Maggi et al. 2015, Thomsen et al. 2016a).

1.2 *Undaria*'s natural distribution and invasion history

The kelp *Undaria pinnatifida* (Harvey) Suringar (hereafter referred to as *Undaria*) has been named as one of the 100 worst invasive species, and is one of the most successful marine invaders worldwide (Lowe et al. 2000, Epstein and Smale 2017, South et al. 2017). *Undaria* is native to the coastal waters of China, Japan, and the Korean Peninsula, where it has been cultivated and harvested for centuries. It is now found around the world on almost every continent. Populations have become established in parts of the Mediterranean Sea, the Atlantic coasts of France, UK, Ireland, Spain, Portugal, and Argentina, the Pacific coast of the USA and Mexico, as well as southern parts of Australia and much of New Zealand's coast (Curiel et al. 2002, Silva et al. 2002, Casas et al. 2004, South et al. 2017). The main vector with which *Undaria* is introduced into new ecosystems is fouling on commercial vessel hulls (reviewed by South et al. (2017). Ballast water is thought to be less important as a vector. In France, it has also been introduced for mariculture purposes (Perez et al. 1984), but to my knowledge intentional introductions did not occur in New Zealand.

In its native range *Undaria* grows from the low intertidal zone to a depth of ca. 18 m, being most abundant in the lower intertidal zone to ca. 3-4 m depth (Kim et al. 1998). The macroscopic stage is easily identifiable with a holdfast, single stipe, and a simple blade with its characteristically prominent midrib, and a large sporophyll from winter to spring (Suárez Jiménez 2015) (Fig. 1.1). *Undaria* has an annual life history, with higher photosynthetic, growth rates and size during the colder months (Campbell et al. 1999). It is able to grow explosively in good conditions at a rate of 1-1.7 cm per day, up to a length of 1.3-2 m (Schaffelke et al. 2005, Schiel and Thompson 2012). In its native range *Undaria* produces its spores in early to mid-spring, and it has been suggested that individuals can survive for up to 2.5 years (Hewitt et al. 2005). In its native range and most invaded countries, *Undaria* is believed to have an annual life cycle and is generally absent mid through late summer (James and Shears 2012, Schiel and Thompson 2012, South et al. 2016). A high propagule

pressure, high longevity of spores and the ability of damaged but attached sporophytes to re-grow means that it is virtually impossible to eradicate from a region once it has become established (Wotton et al. 2004, South et al. 2017).

Figure 1.1. *Undaria* individuals with prominent midrib and large reproductive sporophyll

The effects of *Undaria* appears to vary between regions and associated organisms. In Argentina, *Undaria pinnatifida* has been suggested to reduce native seaweed diversity through competitive effects (Casas et al. 2004) but also increase invertebrate abundance and diversity through habitat provisioning (Irigoyen et al. 2011). In Tasmania, Australia, several studies investigated the establishment of *Undaria* and its potential impacts on native algae (Valentine and Johnson 2003, Johnson et al. 2004, Valentine and Johnson 2005). In these studies *Undaria* did not affect native algae but filled gaps in canopies, rapidly colonizing disturbed sites and eventually declining once native canopy-formers recovered, similar to results by Schiel and Thompson (2012) in New Zealand.

In New Zealand, *Undaria* is classified as an unwanted organism but has nevertheless been permitted for marine farming for selected areas and only under special harvesting conditions since 2010 (MAF 2010). The first record of *Undaria* in New Zealand was in Wellington Harbour in 1987 (Hay and Luckens 1987), and it can now be found in almost all of New

Zealand's international ports and several other ports and surroundings (Russell et al. 2008, South et al. 2017). By 1988, searches of other harbours had confirmed *Undaria*'s presence in Timaru, Oamaru and Lyttelton Harbour the following year (Hay and Luckens 1987). It is prolific on aquaculture mussel lines in the Marlborough Sounds (Chen 2012), and is found on many exposed rocky reefs low in the intertidal zone (Russell et al. 2008).

Once *Undaria* is established, its spread in South Canterbury and Otago has been documented as 1-2 km per year (Russell et al. 2008). In Tasmania, spread rates averaged about 10 km per year (Shepherd and Edgar 2013). Several mechanisms of local dispersal are known (South et al. 2017). Natural dispersal includes spread of spores, drift of unattached sporophytes and movement of sporophytes attached to materials that are moved by waves and currents (Schaffelke et al. 2005, Sliwa et al. 2006), However, human-assisted dispersal with commercial and recreational vessels and movement with aquaculture equipment are common and probably responsible for greater spread rates (Forrest and Hopkins 2013, South et al. 2017).

While extensive research has documented *Undaria*'s distribution, physiology and growth patterns in New Zealand (Hay and Luckens 1987, Thompson 2004, Chen 2012, Schiel and Thompson 2012), there have been few studies on its impact on native ecosystems. Typically, invasive species with high abundance have strong effects on other species (Parker et al. 1999, Thomsen et al. 2011). Given the large biomass of *Undaria* in parts of its invaded range in New Zealand (Thompson 2004, South et al. 2016) and other parts of the world, one would therefore expect substantial ecological impacts, but we currently have only limited and somewhat conflicting knowledge about this.

In New Zealand, a three-year mensurative before-after-control-impact (BACI) study by Forrest and Taylor (2002) found no evidence of displacement of native canopy-forming algal species by *Undaria* in Lyttelton Harbour. Surprisingly, in that study, the presence of *Undaria* apparently led to an increase in the abundance of native sub-canopy algae. However, Forrest and Taylor only sampled algal cover twice a year, once in spring and then again in autumn, and therefore missed the winter months when *Undaria* typically is most abundant (Thompson 2004). The high natural temporal variation in macroalgal abundance in Lyttelton Harbour therefore makes the biannual sampling study by Forrest and Taylor (2002) more open to interpretation and less conclusive.

In another more detailed two-year manipulative removal experiment investigating the effect of *Undaria* on native seaweeds in New Zealand, it was also shown that *Undaria* had little effect on diversity of macroalgae and sessile invertebrates and only a transient impact on the abundance of two inconspicuous native seaweeds (South et al. 2016). This surprisingly low impact was despite that *Undaria* reached canopy cover of up to 100% during the winter months. A biomass assay by South et al. (2016) also showed that *Undaria* had a positive effect on primary productivity, suggesting that the effects of *Undaria* are additive to existing processes, rather than substitutive. These results are supported by the findings of Valentine and Johnson (2003) and Schiel and Thompson (2012), who concluded that rather than replacing existing algal species, *Undaria* recruited mostly into gaps where the native canopy had been disturbed. Although removing the native canopy species increases *Undaria* recruitment, removing sub-canopy species such as coralline turf may actually decrease recruitment, as Thompson (2004) found that *Undaria* recruitment was greatly reduced in Lyttelton Harbour and almost non-existent in Moeraki when coralline turf was removed.

1.3 *Perna canaliculus*

The New Zealand green-lipped mussel, *Perna canaliculus* (Gmelin) 1791 (Bivalvia: Mytilidae), is endemic to New Zealand, found in a variety of habitats ranging from rocky reefs to soft sediment shorelines between the intertidal zone and depths of ca. 50 m (Powell 1979, Marsden and Weatherhead 1999, Fox 2003). It is a filter-feeder and feeds on microscopic algae and other seston (Marsden and Weatherhead 1999). Typical food resources for such filter-feeders are various plankton, bacteria and dead organic matter (Fréchette and Bourget 1985). In the subtidal and lower intertidal zones, these food resources as well as oxygen are continuously provided due to waves and tidal currents (Fréchette and Bourget 1985).

Perna canaliculus (hereafter referred to as *Perna*) occurs where conditions are favourable in terms of wave exposure, occurrence of larvae, substrates for settlement, and food supply (i.e., suitable seston) (Gardner 2000, Gardner and Thompson 2001, Fox 2003). In the intertidal zone, *Perna* is subjected to stress caused by desiccation, high temperature variability, and reduced feeding time (Marsden and Weatherhead 1999). *Perna*, like other mytilids, is attached to rocky substrate by byssus threads and typically occurs in clumps

whereby individuals located in the middle of clumps typically are less affected by abiotic stressors and predation. The habitat preferences of *Perna* and *Undaria* overlap to a large extent, particularly in the upper subtidal zone.

The condition of mussels is usually assessed by a 'condition index' (CI). A wide variety of calculations have been used to calculate CI. Baird (1958) defined a 'wet volume' condition index as the ratio of 100 × wet meat volume (ml) over the difference between whole volume and shell volume. Later versions of CI were based on dry and wet meat and shell weights (i.e., the ratio of 100 × dry meat weight over wet whole mussel weight less shell weight) (e.g., Hickman and Illingworth 1980). Another variation of calculating CI is to use the ratio of 100 × tissue weight over total mussel weight (after draining on filter paper) (Garen et al. 2004). In a recent study (Lander et al. 2012) calculated the CI as the ratio of 100 × dry meat weight over dry shell weight. The use of CI gives the ability to track bivalve growth and health across seasonal variation which makes it particularly helpful for mariculture to evaluate the commercial value of stock (Camacho et al. 1995, Fox 2003, Peharda et al. 2007). Condition index is closely related to seasonal conditions as well as the reproductive cycle of mussels, and will fluctuate according to environmental conditions such as temperature, salinity, and food availability (Fox 2003, Lachowicz 2005). As mussels grow, their soft tissue volume increases but the shell weight increases even more, in relative terms. Therefore, as mussels grow, their CI decreases slightly.

Reproduction requires large amounts of energy for gametogenesis and spawning, and this appears to be reflected in seasonal changes in CI. Studies on the CI of *Perna* report different results regarding seasonal differences. In a study replicated in central New Zealand (Wellington Harbour and Marlborough Sounds) and northern New Zealand (Northland and Great Barrier Island), CI tended to be highest in spring and summer and lowest in winter (Hickman and Illingworth 1980). However, this pattern was less clear at the central New Zealand sites, and there was much variability from month to month (Hickman and Illingworth 1980). There also appears to be considerable differences between locations related to latitude and water temperature. A study by (Fox 2003) in the Marlborough Sounds concluded that *Perna* flesh weight is lowest in winter, around the time of year when the proportion of mussels with mature gonads declined, apparently following spawning. However, Hickman and Illingworth (1980) state that spawning of *Perna* may occur

throughout the year but with peaks in spring to early summer and autumn, which suggests that there is no clear link between spawning and a decline in CI. In Europe, differences in the season when CI declines were also observed in *Mytilus* spp. For example, in different regions of the Mediterranean sea, the lowest CI values in *Mytilus galloprovincialis* occurred in September or December (Orban et al. 2002). In Scotland, a low CI in *Mytilus edulis* coincided with spawning in winter (Okumuş and Stirling 1998).

Several environmental factors can affect mussel CI. For example, under high nutrient conditions, abiotic environmental factors (water temperature, salinity) were more closely related to CI than nutrient availability (Hickman et al. 1991). However, a minimum food level was identified, where concentrations below 200 µg carbon per litre resulted in a sharp decline in CI (Hickman et al. 1991). It is unclear how much of an impact epibiotic seaweeds, such as *Undaria*, might have on mussel CI.

1.4 Mussels as habitat formers and ecosystem engineers

Mussels and other bivalves are important ecosystem engineers that increase habitat complexity and make habitats more suitable for other species (Gutiérrez et al. 2003, Borthagaray and Carranza 2007, Buschbaum et al. 2009, Bateman and Bishop 2017). For example, a meta-analysis by Bateman and Bishop (2017) found that, overall, the presence of bivalves led to an increase in both species density and species abundance of mussel-associated invertebrates. However, in this analysis the effect of mussels was more context-dependent compared to other bivalves such as oysters and pinnids, perhaps because mussels create a more homogeneous habitat compared to oyster reefs or pinnid shells, or because impact data exist for a variety of different mussel-dominated habitats, including both sedimentary estuaries and rocky reefs. This review also highlighted that very few research papers have tested, with manipulative experiments, for impact of mussels on rocky shore organisms (see (Bertness et al. 2004, Valdivia and Thiel 2006, Silliman et al. 2011, Lemieux and Cusson 2014) for rare examples).

In an experiment comparing high and low mussel abundances (20% of mussels were removed three times over four weeks), plots with fewer mussels had different a community structure and lower richness, but similar abundances, of sessile invertebrates, compared to

plots with more mussels (Valdivia and Thiel 2006). Furthermore, removal treatments had no effect on mobile or semi-sessile invertebrates or richness or abundance of algal species. Species with low mobility and poor abilities to cling to the substratum were most affected by mussel removal (Valdivia and Thiel 2006). Where mussels are removed, some algal species, such as the small kelp *Postelsia palmaeformis*, can recruit onto the new bare rocky space (Paine 1979). Another intertidal study found that, although mussels feed on algal spores, there was still higher abundance of some algal species under live mussels in the intertidal zone, compared to empty shells or no mussel cover, probably because desiccation stress was reduced in this microhabitat (Santelices and Martinez 1988). A study in Uruguay found significantly higher richness of (particularly sessile) invertebrate species in areas with high mussel cover compared to areas without mussels (Borthagaray and Carranza 2007). There was also a positive relationship between the abundance of mussels and the abundance of invertebrates within mussel patches. Finally, in Patagonia, Argentina, a region characterized by strong dry winds, and therefore extreme intertidal desiccation stress, mussels facilitated an entire invertebrate community, resulting in 20 times higher diversity in areas where mussels were present compared to neighbouring primary substratum (Silliman et al. 2011). With the exception of limpets and barnacles, invertebrates were found almost exclusively associated with mussels. Contrary to these studies, Lemieux and Cusson (2014), found no difference between artificially created assemblages of mussels and fucoid seaweeds on the total abundance or diversity of the associated species between these different assemblages of habitat-forming species.

1.5 How seaweeds affect mussels

Several studies have quantified interactions between mussels and the large canopy-forming seaweeds that potentially can attach directly onto mussel shells (Dittman and Robles 1991, Laudien and Wahl 1999, O'Connor et al. 2006). For example, it is possible that attached seaweeds (in addition to other epibiota like barnacles or hydrozoans), reduce mussel mortality through visual and physical obstruction of predators such as starfish (Laudien and Wahl 1999). However, attached fucoid seaweeds have also been found to double the mortality of mussels on a rocky shore in Ireland, especially during storm events due to increased hydrological drag (O'Connor et al. 2006). Even if mussels are not torn off the

substrate, when large algae are attached mussels may increase production of energetically expensive byssal threads (to increase their probability of survival during storms), which probably decreases their growth rate (Thieltges and Buschbaum 2007). This hypothesis was supported by Dittman and Robles (1991) who found that overgrown mussels had significantly lower growth and reproductive rates. Nevertheless, Dittman and Robles (1991) did not examine the underpinning mechanisms behind these impacts but suggested that, in addition to energetic cost from increased byssal production, reduced growth rate may also be due to epibiota obstructing mussel temperature regulation because epibiota also reduce surface reflectance and increase evaporative cooling (Dittman and Robles 1991).

Furthermore, epibiotic species could hamper the feeding abilities of their host species in several ways. Fouling species can limit the ability of hosts to move and position themselves to reach the best feeding conditions (Thieltges 2005). In mussel reefs, especially when found on soft sediments, any reduced mobility resulting from being overgrown by epibiota may increase the risk of being buried (or partially buried), which would affect their ability to feed. Moreover, if mussel hosts and their epibionts occupy similar niches they may compete for resources (e.g. Riera et al. 2002), although in that particular study competition effects were found to be of minor importance. The American slipper limpet *Crepidula fornicata* is a filter-feeder similar to the mussel *Mytilus edulis* on which it is often found attached. It has even been observed preferentially positioning itself with feeding openings close to the mussels siphon (Thieltges 2005), where *Crepidula* may use the current created by the mussel to increase its own filtration. Similarly, barnacle fouling can also reduce growth in mussels (Buschbaum and Saier 2001). However, this inhibitory effect contrast an earlier study by Laihonen and Furman (1986) who found no effect on the host mussels themselves, even though barnacles attached to live mussels had increased growth rates compared to barnacles attached to empty shells.

In soft sediment habitats epibiota can increase sediment accumulation (Albrecht and Reise 1994). For example, sediment depth was three times greater when the fucoid *Fucus vesiculosus* was attached to *Mytilus edulis*, than in areas where *F. vesiculosus* was absent. Not only did this result in an increase in the proportion of the mussels being buried in sediment, it also changed their clumping behaviour. In the absence of *F. vesiculosus*, *M. edulis* forms epibenthic garlands, often 2-3 mussels in height. By contrast, in the presence of

the epiphytic algae, *M. edulis* forms a singular layer of mussels sunk into the mud. Interestingly, without mussels providing attachment substratum, there would be no algae present in this sedimentary ecosystem. Another study by Albrecht (1998) found that *M. edulis* facilitated a different type of ephemeral green algal species, but only in the absence of the dominant algal grazer, *Littorina littorea*.

1.6 *Undaria*'s impacts on rocky shore ecosystems

Perna grows naturally in many of the same areas where *Undaria* has established permanent populations (Buchanan and Babcock 1997). *Perna* is one of the main aquaculture exports of New Zealand, comprising 75% of the total aquaculture export. In 2011, 100,000 tonnes of *Perna* were exported, with a total value of 240 million USD. *Perna* is highly valued compared to other mussel species as it is larger than many overseas species and is prized for its high volume of meat. Qualitative observations suggest that *Undaria*, like many other seaweeds, can grow on or around mussel reefs in close association with *Perna*, and potentially also settle directly onto the mussels (Woods et al. 2012). Similarly it has been noted that *Undaria* often is found on or around New Zealand aquaculture mussel farms (pontoons, ropes, boys) (Chen 2012, James and Shears 2012, Fletcher 2013). In New Zealand, Fletcher (2013) observed that although the invasive ascidian *Didemnum vexillum* was the dominant fouling species on *Perna* on marine farms in the Marlborough Sounds, other fouling species such as the blue mussel, *Mytilus galloprovincialis* and *Undaria* were also commonly observed, and may contribute to the observed negative effects on mussel density and loss. Despite the importance of *Perna* as a reef-forming organism, as a major export aquaculture product, and the continued expansion of *Undaria* to more mussel reefs and mussel farms, no study (neither in New Zealand or abroad) has quantified ecological interactions between *Undaria* and mussels.

Mussels are often host to a variety of epibiotic flora and fauna. It is not uncommon to find barnacles (Cirripedia), limpets (Patellidae and other limpets-like gastropods), tube worms (Canalipalpata), and any number of other animals growing on their surface (Wahl 1989, Woods et al. 2012). Some algal species, such as encrusting coralline algae (e.g., *Lithophyllum* paints and *Corallina officinalis*), will also settle onto mussels. Less frequently, larger algal

species, *Undaria* among them, will settle on to mussels (Albrecht and Reise 1994, Fletcher 2013).

Despite records of co-occurrences, I am not aware of any scientific studies that have studied interactions between *Undaria* and mussels in New Zealand. However, (Battershill et al. 1998) found mixed invasion impacts on the understorey community. There was an apparent reduction in *Carpophyllum* spp. algae, lower cover of *Corallina officinalis* and turfs in Wellington Harbour, but an increase in species diversity of algae, molluscs and echinoderms in Queen Charlotte Sound *(Dean 1999, Schaffelke and Hewitt 2007)*.

1.7 Overview and aims of this thesis

This thesis contains a general introduction (Ch.1), a discussion (Ch. 5), and three data chapters (Ch. 2-4) where I examine relationships between *Undaria*, *Perna*, and mussel-associated algal and invertebrate communities.

Ch. 2: Distribution of *Undaria* and mussels in Lyttelton Harbour

In chapter 2 I analysed distribution patterns of *Undaria* throughout Lyttelton Harbour and potential co-occurrences with native mussels. This was achieved through reanalysing a previous harbour wide survey at 20 sites and 2 tidal levels, performing a long term repeated survey and a small-scale attachment substrate survey at Pile Bay. In this chapter I hypothesized that (1) *Undaria* will be more abundant in association with mussels than in areas where mussels are absent because they prefer similar environmental conditions (tidal level and wave exposure among others), and that (2) *Undaria* will exhibit reduced seasonal variation when associated with mussel reefs, as the microhabitat may facilitate more persistent mature *Undaria* populations.

Ch. 3: Effects of *Undaria* on condition of *Perna* and mussel epibiota

Undaria individuals may sometimes be attached directly to mussels so in chapter 3 I investigated whether *Undaria* affects the condition index of their mussel hosts. Epibiota

have been shown to negatively affect mussel condition but effects of epibiotic *Undaria* is unknown. Here I quantified if and how *Undaria* affected (1) *Perna* itself (condition index), (2) other sessile epibiota directly attached to mussels, and (3) large mobile invertebrates associated with mussels. These data were obtained through 19 monthly collections of individual mussels with and without attached *Undaria*. I hypothesized that *Undaria* has a negative impact on mussel condition index and on other sessile epibiota (through competition for space) but positive effects on mobile invertebrates (through habitat-provisioning).

Ch. 4. Effects of *Undaria* and mussel removals on *Undaria* recruitment and algal and invertebrate community composition

In Chapters 2 and 3 I show that *Undaria* and mussels co-exist on natural reefs. I therefore, in Chapter 4, carried out a two-factorial removal experiment (with repeated removals over one year and follow-up community sampling after 10, 15, and 25 months) to determine whether the presence of *Undaria* and *Perna* affect recruitment of each other or community composition of mobile invertebrates of sessile invertebrates and alga. I hypothesize that (1) mussels increases *Undaria* recruitment (through stress-reduction), (2) *Undaria* limit mussel recruitment (through space occupation) and (3) the that algal and invertebrate communities differ between plots where *Undaria* and *Perna* have been removed compared to un-manipulated control plots.

1.8 Study site

Figure 1.2. Photo of the rocky intertidal reef at Pile Bay, Lyttelton Harbour, New Zealand. Dense beds of mussels and *Undaria* can be seen in the low-intertidal zone.

All surveys and experiments were performed in Lyttelton Harbour (-43.609520 S, 172.760411 E), which occupies ca. 43 km^2 of a volcanic crater on the north side of the Banks Peninsula, along the east coast of the South Island of New Zealand. The maximum tidal range is 1.9 m and the sea surface temperatures typically vary between 8°C in July to 20°C in February (Lilley et al. 2016). The surveys and sampling performed at Pile Bay were undertaken on a rocky intertidal reef between Pile Bay and Deep Gully Bay (-43.617993 S, 172.765748 E) on the southern side of Lyttelton Harbour, Canterbury, at (Fig. 1.2, Fig. 1.3). This reef consists of a basaltic platform and interspersed boulder fields with medium to large boulders. It is a semi-exposed reef with swells of 0.5-1.2 meters, occasionally larger than this during storm events. The study was performed in the intertidal zone at approximately 0.3 m above lowest astronomical tide, where the reef generally has a base layer of coralline turf (*Corallina officinalis* (L.)), with stands of fucoid and laminarian algae, interspersed dense mussel beds and patches of bare rock. The dominant algal species from the intertidal–

subtidal fringe downwards on the reef are the fucoids *Hormosira banksii* ((Turner) Decaisne) and *Carpophyllum maschalocarpum* ((Turner) Grev.), and laminarian algae *Ecklonia radiata* (J. Agardh, 1848) and *Macrocystis pyrifera* ((L.) Agardh). Both green lipped mussel (*P. canaliculus*) and blue mussels (*M. galloprovincialis* (Lamarck, 1819)) are present on the reef, with higher abundance of *Perna* toward the eastern end of the peninsula and increasing abundance of *M. galloprovincialis* toward the western side of the peninsula.

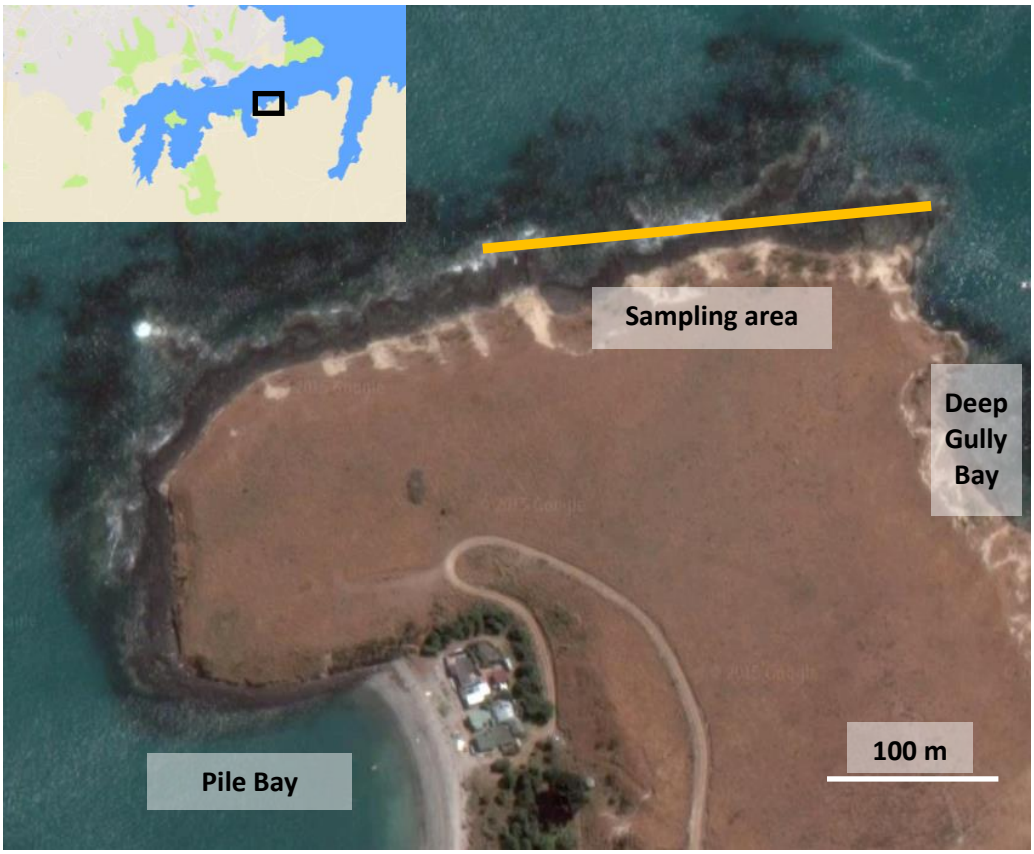

Figure 1.3. Satelite photo of the Pile Bay reef sampling area, and its relative position in Lyttelton Harbour, New Zealand

2 Distribution and abundance of *Undaria pinnatifida* in Lyttelton Harbour and its co-occurrence with native mussels

Abstract

Non-native species have invaded coastal systems worldwide, altering community structures and ecosystem functioning. One of the most widely distributed marine invaders is the kelp *Undaria pinnatifida*. *Undaria* is an annual kelp that typically has a unimodal winter-dominated growth pattern. Despite being a large and abundant invader on rocky reefs and mussel farms, no studies have examined to what extent *Undaria* co-occurs with mussels on rocky reefs and what the potential ecological implications of *Undaria*-mussel interactions are. Here, I examined whether *Undaria* and mussels co-occur on rocky reefs in Lyttelton Harbour, New Zealand, at different spatial and temporal scales. I performed surveys of *Undaria* and mussel abundances Harbour wide in the low and mid-tidal zones, repeated photo surveys at a reef at Pile Bay at different times of the year, and a survey of the attachment substrates of *Undaria* individuals. I found that *Undaria* is often associated with, or even directly attached to, mussel aggregations in the low intertidal zone. While I did observe seasonal variation in *Undaria* abundance, there was less variation between the winter peak and summer senescence seasons, and consistently higher cover of *Undaria* when it was associated with mussel aggregations than when it was not. My findings suggest that the pattern of sustained seasonal presence of *Undaria* may be due to overlapping generations and longer growing seasons, rather than individual plants persisting for an increased length of time. The presence of mussels and the higher wave energy at locations where mussels typically occur may reduce environmental stressors (such as desiccation and grazing) that affect *Undaria*, thus probably increasing the recruitment, growth and survival of *Undaria*. This is an interaction that has not been documented before, and it demonstrates that relationships between invading species and native habitat-forming species may be important. These findings are important for our understanding of the ecology of marine invasions, and they have applied implications for the management of *Undaria* and other invasive species.

2.1 Introduction

The effects of invasive species have been well documented, but even with increasing border control measures, it is difficult to completely prevent the arrival of new potentially harmful species. While the arrival and establishment of many terrestrial species is being prevented by measures such as banning high-risk goods and fumigating cargo (Ormsby and Brenton-Rule 2017), it is more difficult to prevent the establishment of marine invasive species. Marine species can be introduced to new areas through hull fouling of seagoing vessels, being transported in ballast water, or through the aquarium trade. Approximately 20% of the 100 worst invasive species in the world are fish, aquatic invertebrates, and aquatic plants (Lowe et al. 2000).

Many governments across the world have established lists of marine pests and potential marine invaders based on species invasion history and likelihood of arrivals and establishment (Molnar et al. 2008, Champion et al. 2014). Invasive species can have significant ecological impacts, changing the structure of existing communities and the ecological services provided by native species (Clavero and Garcia-Berthou 2005, Didham et al. 2005, Molnar et al. 2008, Thomsen et al. 2009). Moreover, introduced species can create economic losses as they may interfere with agricultural and aquaculture systems and decrease export value (Pimentel et al. 2005, Kluza et al. 2006, Howes et al. 2007, Katsanevakis et al. 2014).

Undaria's invasion history

The kelp *Undaria pinnatifida* (hereafter '*Undaria*') is a highly successful marine invader (Lowe et al. 2000, Pereyra et al. 2014, South et al. 2017). *Undaria* is native to the coastal waters of China, Japan, the Korean Peninsula, and Pacific Russia, where it has been cultivated and harvested for centuries as a food and pharmaceutical resource (Saito 1975). *Undaria* is now found around the world on almost every continent with established populations in parts of the Mediterranean Sea, the Atlantic coasts of France, UK, Ireland, Spain, Portugal, and Argentina, the Pacific coast of the USA and Mexico, as well as southern parts of Australia and much of New Zealand's coast (Curiel et al. 2002, Silva et al. 2002, Casas et al. 2004, South et al. 2017).

Undaria was first detected Wellington in New Zealand in 1987 (Hay and Luckens 1987), and can now be found in almost all of New Zealand's international ports and several other ports and surroundings (Russell et al. 2008, South et al. 2017). The first record of *Undaria* in Lyttelton Harbour was in 1989 (Hay and Luckens 1987). It is prolific on aquaculture mussel lines (of green lipped mussel, *Perna canaliculus*) in the Marlborough Sounds (Forrest and Blakemore 2006, Chen 2012), and is found on many exposed rocky reefs low in the intertidal zone (Russell et al. 2008, Schiel and Thompson 2012, Thompson and Schiel 2012, South et al. 2016). The rate at which *Undaria* is able to spread by itself varies between regions. In South Canterbury and Otago it has been documented as spreading between 1-2 km per year (Russell et al. 2008). By contrast, in Tasmania, spread rates averaged about 10 km per year (Shepherd and Edgar 2013). Several mechanisms of local dispersal are known (South et al. 2017). Natural dispersal includes spread of spores, drift of unattached sporophytes and movement of sporophytes attached to materials that are moved by waves and currents (Schaffelke et al. 2005, Sliwa et al. 2006). However, human-assisted dispersal with commercial and recreational vessels and movement with aquaculture equipment are common and probably responsible for greater spread rates (Forrest and Hopkins 2013, South et al. 2017).

Undaria on mussel reefs

Most of the literature about the invasion history of *Undaria* has focused on its ability to invade, and its effect on, rocky intertidal reefs dominated by turf or encrusting algae and with sparse macroalgal canopies. In addition, *Undaria* has been recorded growing on aquacultural mussel lines (Forrest and Blakemore 2006, Chen 2012) but potential co-occurrence patterns between *Undaria* and mussels in natural mussel habitats has not been investigated. In Lyttelton Harbour on the South Island of New Zealand, the two most common mussels are *Perna canaliculus* and *Mytilus galloprovincialis* (hereafter *Perna* and *Mytilus*, respectively). They are mainly found on more or less exposed rocky reefs, and sometimes also on soft sediment shorelines, between the intertidal and depths of ca. 50 m (Powell 1979, Marsden and Weatherhead 1999, Fox 2003). Especially in the upper subtidal and lower intertidal zones, the habitat preferences of *Perna* and *Undaria* appear to overlap, whereas in the mid-intertidal, both mussels and *Undaria* are likely restricted vertically by

desiccation stress (Kennedy 1976, Bollen et al. 2017). *Perna* and *Undaria* also appear to have similar preferences for wave exposure (James and Shears 2016b). Furthermore, it is possible that the presence of *Perna* facilitates the establishment and growth of *Undaria* as *Undaria* can be found growing on *Perna* (Chen 2012, James and Shears 2016b, South et al. 2017). To date no comprehensive survey has been undertaken to determine to what extent *Undaria* and mussels co-occur, and how widespread the two species are found together on natural reefs across a larger area such as Lyttelton Harbour.

Undaria is typically characterized as an annual species in both its native and invasive range, with a distinct hiatus over summer when its macroscopic form is absent, and with major differences in abundance and cover in its growth vs. senescence/hiatus seasons (Hay and Villouta 1993, Morita et al. 2003, Thompson and Schiel 2012, James et al. 2015, James and Shears 2016a, South et al. 2016, South and Thomsen 2016). This 'transient' phenology, with a distinct abundance and cover peak in late winter, may at least partially explain why past studies have found relatively low impacts on native species (Forrest and Taylor 2002, South et al. 2016, South and Thomsen 2016). Importantly, the majority of these studies have been done in shallow (< 4 m depth) rocky reefs dominated by seaweed and have therefore focused on effects of *Undaria* on native algae. However, my personal observations and a recent study (James and Shears 2016a) suggest that this pattern may be less distinct than typically portrayed. For example, *Undaria* has been shown to have relatively sustained high abundances on subtidal artificial mussel lines (James and Shears 2016b) and can sometimes be found on native reefs in association with mussels in high abundance even outside of *Undaria*'s normal growing season.

Study aims and hypotheses

In this study I examined the distribution of the invasive kelp *Undaria pinnatifida*, around Lyttelton Harbour, New Zealand, the degree to which it exists in association with mussels, and its frequency on different types of substrate on which it is commonly found on or around native mussel reefs.

I hypothesised that:

(i) *Undaria* will be present at all rocky reefs in Lyttelton Harbour because it has been present in parts of the Harbour for many years and because it has effective dispersal mechanisms;

(ii) *Undaria* will be more abundant in association with mussels than in areas where mussels are absent, partly because they prefer similar environmental conditions (e.g. relatively similar tidal levels and wave exposure levels), and partly because mussels may reduce stress and facilitate *Undaria* settlement (for example, by reducing desiccation and predation); and

(iii) *Undaria* will be attached to mussels in areas where they are both in high abundances, as *Undaria* has been shown to settle onto most hard surfaces, and mussels increase the available attachment area on the reef.

2.2 Methods

Three datasets were used to address my objectives: a larger-scale survey of 20 reefs across Lyttelton Harbour, a photo survey of temporal changes in *Undaria* and mussel cover at my main study site at Pile Bay, and a survey of substrates to which *Undaria* is attached at Pile Bay.

Lyttelton Harbour survey

In order to quantify spatial patterns of *Undaria* and mussel occurrence, I re-analysed the data from a survey of the low and mid tidal zones of 20 intertidal rocky reefs (Fig 2.1) that was carried out between May and November 2015 (see Lilley et al. 2016 for more detailed information on each reef). These data were collected for the Regional Council (ECAN) to evaluate sediment effects on biological communities, and they have not previously been analysed for *Undaria*-mussel co-occurrence patterns. Sites were sampled on spring low tides by laying out a 30 m transect parallel to the water line. Ten 0.5 $\times$ 0.5 m quadrats were haphazardly placed along each transect and were separated by at least 1 m. Within each quadrat, the percentage cover of *Undaria* and all mussels (by combining the abundances of

two dominant mussel species, *Perna canaliculus* (97%) and *Mytilus galloprovincialis* (3%)) was quantified with a minimum resolution of 0.1%.

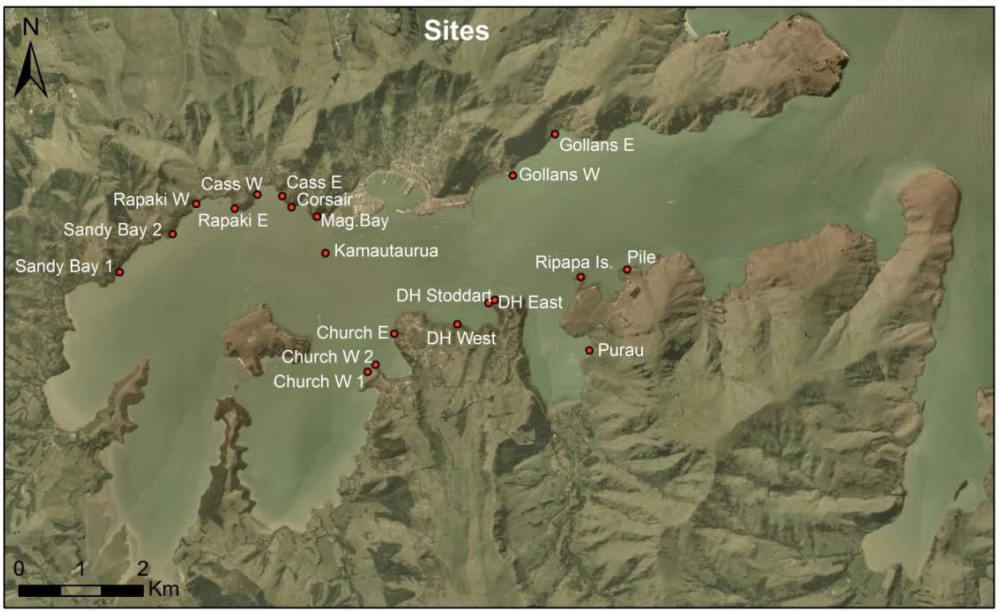

Figure 2.1. Satellite Photo of Lyttelton Harbour, New Zealand, and the location of the 20 sites surveyed in Lilley et al. (2016), that were used in the analysis.

The effect of sample site on *Undaria* cover, *Undaria* count, and total mussel cover was analysed with ANOVA. Differences in *Undaria* cover, *Undaria* count, and total mussel cover between the northern and southern sides, and the eastern and western halves of the harbour were examined by a 2-way ANOVA. To determine whether the amount of mussel cover had an effect on the level of *Undaria* cover I performed linear regression on both the raw data and $\log_{10}$ transformed data.

Pile Bay temporal survey

To quantify temporal patterns of mussel and *Undaria* co-occurrences, the Pile Bay reef (-43.619408, 172.762279) in the outer Lyttelton Harbour was surveyed on nine different months between June 2015 and November 2017. Percent cover of *Undaria* and mussels were quantified from 1886 digital photos (Fig. 2.2), each covering 1 m^2 of the reef (Fig. 1.2, 1.3). Photos of the 1 m^2 plots were taken during spring low-tide in the low and mid-intertidal zones (including tide pools). Plots were haphazardly positioned along a zigzagged transect

line from low-to-mid-to-low elevation covering ca. 700 m of rocky reef. Plots were separated by at least 1 m. This photo-survey was used because it allowed rapid sampling of a much wider spatial area during the very short extreme low tides when mussels and *Undaria* were emerged (by comparison, only a fraction of this area could have been sampled with standard counting of frames). This method provides solid data for rapidly growing large canopy-forming alga like *Undaria* and of mussels generally, but will underestimate mussel abundances when completely covered by *Undaria*. Note, however, that (a) *Undaria* virtually never covered the entire 1 m^2 of photos, (b) mussels were still visible on photos where *Undaria* occurred in high abundances and (c) any potential underestimation of mussel abundances, work against my working hypothesis and my tests is therefore conservative (i.e., if I still find support for my hypothesis, the real effect sizes may actually be greater).

Figure 2.2. Example of a photo used to assess percent cover of *Undaria* and mussels in plots each covering ca. 1 m^2 of the reef.

The abundance of *Undaria* and mussels was quantified on six occasions in the period of high *Undaria* growth (winter to spring: June 2015, July 2016, August 2016, November 2016, December 2016, and September 2017) and on three occasions from *Undaria*'s senescent or absent period (late-summer to early autumn: April 2016, January 2017, and March 2017). These two periods correspond to *Undaria*'s typical growth vs. hiatus phenology in New Zealand (Hay 1990, Hay and Villouta 1993, Schiel and Thompson 2012, Thompson and Schiel 2012, Tait et al. 2015, James and Shears 2016a, b, South et al. 2016, South and Thomsen 2016, South et al. 2017) and are therefore also referred to as the 'expected presence' and 'expected absence' periods. Prior to statistical analysis each photo was classified as 'very low' or 'medium-to-high' mussel cover, where cover was considered to be medium-to-high when it was greater than 10% in the 1 m^2 sample. I used this 10% threshold to have adequate sample sizes for the 'medium' mussel treatments (mussels do generally not dominate in Pile Bay or on other reefs in Lyttelton Harbour, so using a higher threshold resulted in much fewer samples in the 'medium' cover treatments). Analyses using larger or smaller thresholds did not change the main results (unpubl. analysis.).

The data from the photo survey had highly heterogeneous variances (and variances could not be transformed to homogeneity) so could not be analysed by a standard ANOVA. I therefore used Wilcoxon signed-rank tests to examine whether there was a difference in *Undaria* and mussel cover between the *Undaria*'s expected presence and absence seasons, and between plots with low and high mussel cover. Post hoc Wilcoxon tests were performed for *Undaria* cover to further investigate the patterns found.

Undaria attachment survey

To determine the proportion at which *Undaria* was physically attached directly to mussels or other surrounding reef substrates I identified the attachment substrate of 100 randomly selected *Undaria* holdfasts on two 5x5 m mussel dominated rocky headland, in Pile Bay in August 2017. Half of the *Undaria* holdfasts at each headland were sampled at the wave-exposed end, and the other half were sampled at the wave-sheltered base of the headland (coves). The length of each *Undaria* individual was measured to nearest mm and the substratum underneath the centre of its holdfast was characterized as either a mussel, bare

rock and encrusting algae, or turfing coralline algae. *Undaria* attached to mussels may be attached to other sessile epibiota growing on the mussel, rather than directly to the mussels themselves, but potential multi-layered attachments were not quantified here.

To determine whether there was a significant difference between the size of sampled *Undaria* individuals I performed a 3-way ANOVA using sample site, wave exposure, and substrate type as factors. Chi-square analysis was then performed to determine whether the *Undaria* attachment substrate type was dependent on sample site or wave exposure.

All data were analysed using the Excel data-analysis tool pack and R version 3.4.3 (RCoreTeam 2017) and RStudio Version 1.1.383 (RStudioTeam 2016).

2.3 Results

Lyttelton Harbour survey

Both *Undaria* and mussels were almost entirely absent in the mid-intertidal zone in all regions of Lyttelton Harbour, with the average cover being less than 2% in all cases. Because of this I focused on the relationships between *Undaria* and mussels in the low-intertidal zone. There was a significant effect of sample site on the cover of *Undaria* ($p<0.001$) and total mussel cover($p<0.001$) (Table 2.1, Fig 2.3). The sites with the highest average low-intertidal zone *Undaria* cover were Pile Bay, Ripapa Island, and Diamond Harbour West with 59%, 52%, 35% *Undaria*, respectively. The first two being on exposed reefs in the south-east sector, and the latter being on a relatively exposed reef in the south-west sector. The sites with the lowest *Undaria* cover were Magazine Bay, Purau Bay, and Rapaki Bay, which all had average cover of less than 2%. All of these sites with low cover are relatively wave-sheltered bays in the north-east sector of the Harbour. Total mussel cover was highest at the Gollans Bay West, Gollans Bay East, and Ripapa Island sites, with 83%, 64%, and 30% mussel cover respectively. All three sites being in the eastern half of the Harbour. Church Bay, Cass Bay, Sandy Bay, Purau Bay, Rapaki Bay, and Pile Bay, all had total mussel cover of less than 1%.

Table 2.1. One-way ANOVA testing for effect of sample site on the cover of *Undaria* and mussels. Degrees of freedom: Site = 19, residual = 180. Significant results are in bold.

Response	Test factor	SS	F	p
Undaria cover	Site	58048	10.55	**<0.001**
	Residual	52109		
Mussel cover	Site	96358	32.91	**<0.001**
	Residual	27736		

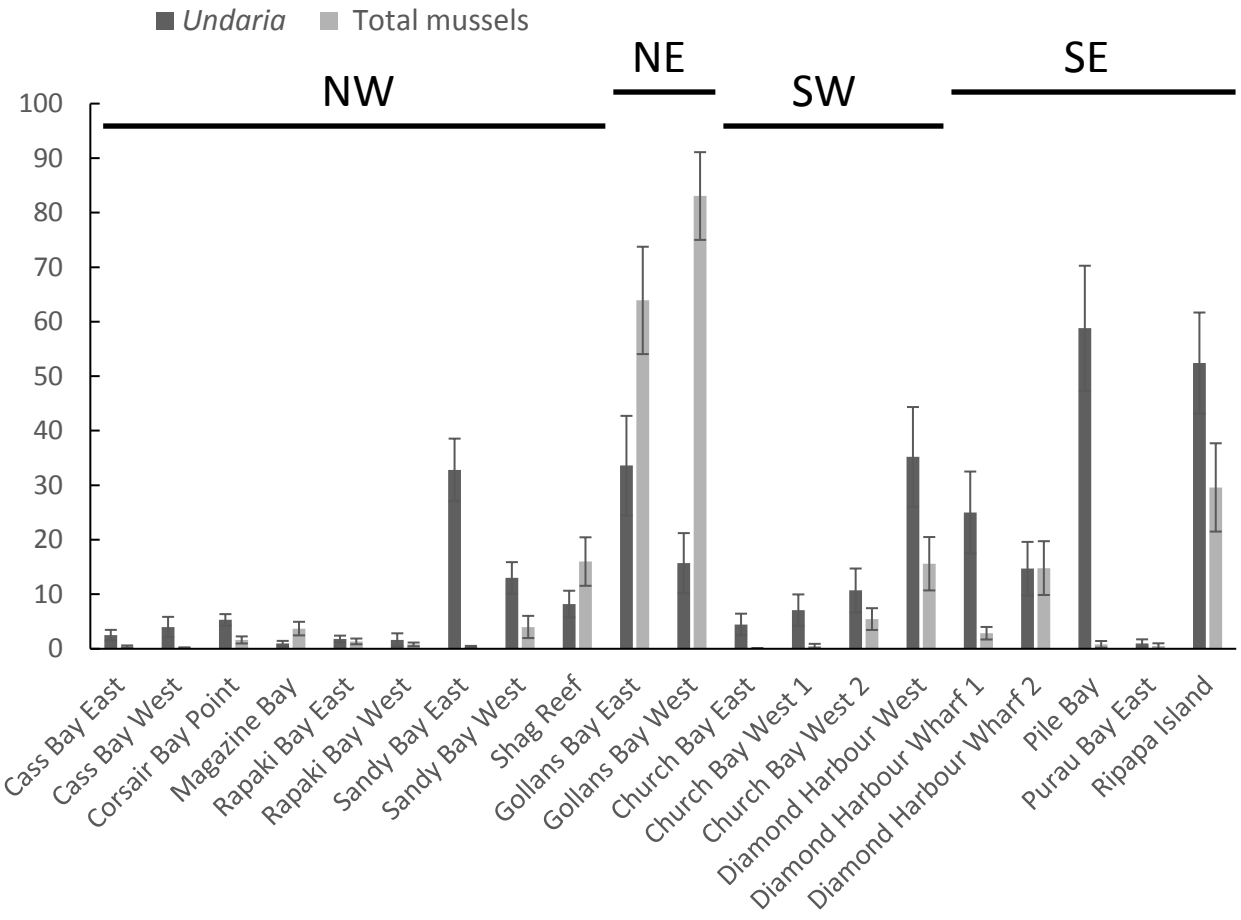

Figure 2.3. Average cover of *Undaria* and mussels in the low-intertidal zone at the 20 reefs surveyed, across the compass regions of Lyttelton Harbour (n = 10 per reef). Bars = 1 SE.

There was a significant difference in *Undaria* count between tidal levels with an average count of 4.6 in the low-intertidal zone and 0.05 in the mid-intertidal zone ($p<0.001$) (Table 2.2, Fig. 2.4a). Within the low-intertidal zone there was a significant difference in the

number of *Undaria* individuals between both the north / south aspect ($p<0.001$), and the east/west aspect of the Harbour ($p<0.001$). The number of *Undaria* individuals was higher on the southern side of the Harbour (6.1 ± 0.8) than the northern side (3.3 ± 0.4) and higher on the eastern side (8.3 ± 1.0) than the western half of the Harbour (2.6 ± 0.3). There was no significant interaction between the E-W and N-S aspects ($p=0.51$). *Undaria* cover data generally mirrored count data: there was a significant difference between *Undaria* cover between the low and mid-intertidal zones ($p<0.001$) with an average cover of 16.4% in the low-intertidal zone, and 0.04% in the mid-intertidal zone (Table 2.2, Fig. 2.4b).

Table 2.2. ANOVAs testing for effects of tidal zone, north/south and east/west site location, on the number of *Undaria* individuals, and the cover of *Undaria* and mussels. Degrees of freedom: Tidal level = 1, North/South = 1, East/West = 1, North/South × East/West = 1, residual = 196. Significant results are highlighted in bold.

Response	**Test factor**	**SS**	**F**	**p**
Undaria count	Tidal level	2070.2	112.06	**<0.001**
	Residuals	7352.7		
Undaria count	North/South	392.8	13.24	**<0.001**
	East/West	1102.3	37.16	**<0.001**
	North/South × East/West	12.9	0.43	0.511
	Residuals	5814.2		
Undaria cover	Tidal level	26910	97.18	**<0.001**
	Residuals	110207		
Undaria cover	North/South	7603.8	16.16	**<0.001**
	East/West	10336	21.97	**<0.001**
	North/South × East/West	6.48	0.013	0.907
	Residuals	92211		
Mussel cover	Tidal level	13854	44.34	**<0.001**
	Residuals	124363		
Mussel cover	North/South	3282.7	16.30	**<0.001**
	East/West	40270	199.93	**<0.001**
	North/South × East/West	41063	203.86	**<0.001**
	Residuals	39479		

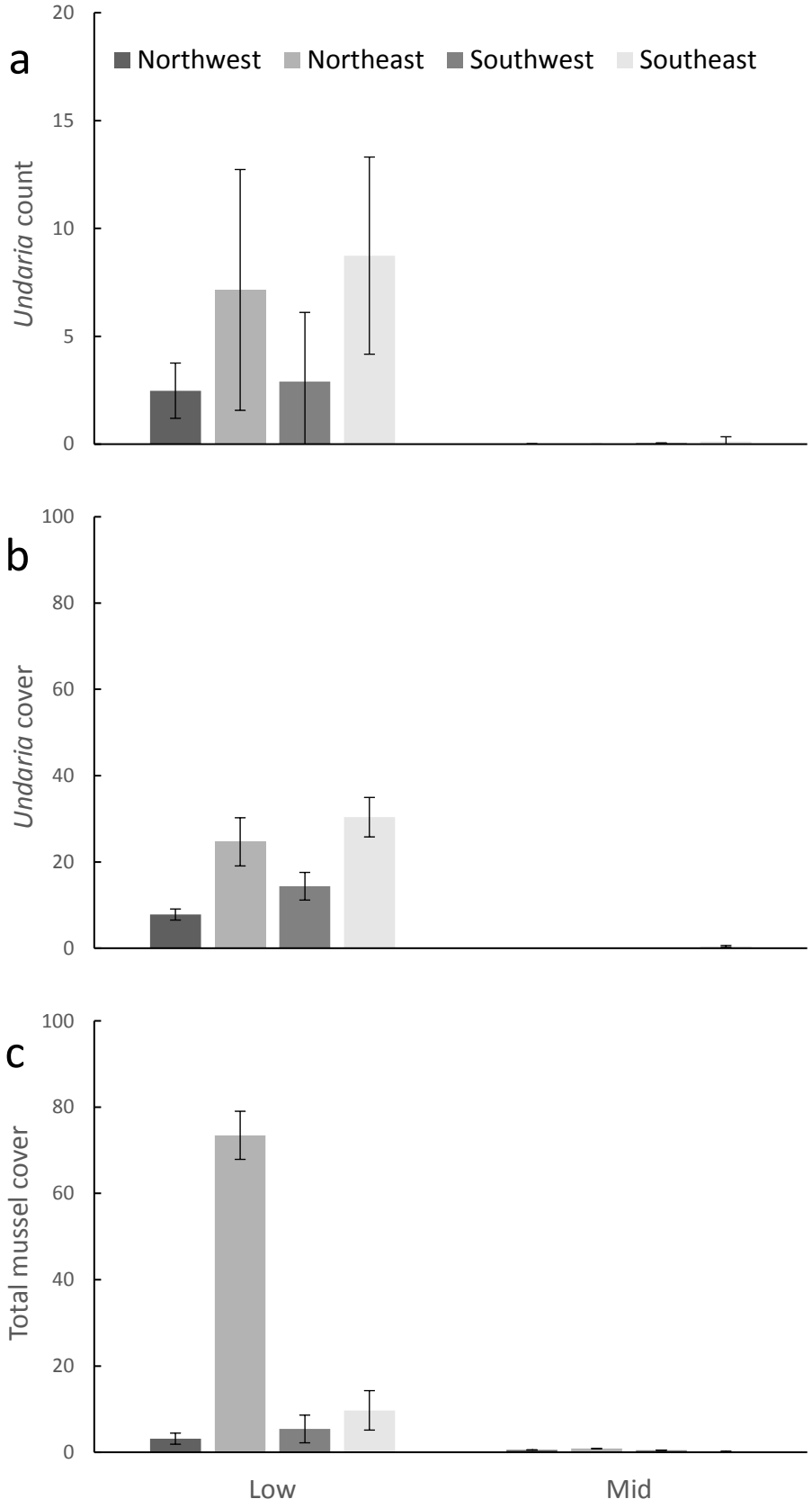

Figure 2.4. Average number of *Undaria* individuals (a), and percent cover of *Undaria* (b) and mussels (c) in low-intertidal zone of the four sectors of Lyttelton Harbour (n = 20 to 90). Bars = 1 SE.

Within the low-intertidal zone there was a significant difference between both the northern and southern sides ($p<0.001$), and the eastern and western sides of the Harbour ($p<0.001$). *Undaria* cover was higher on the southern side of the Harbour (23.3 ± 3.0) than the northern side (10.9 ± 1.6) and higher on the eastern side (28.7 ± 3.6) than the western half of the Harbour (9.8 ± 1.3). There was no significant interaction between the two aspects ($p=0.91$).

Mussels shared the same pattern as *Undaria* around the Harbour, with higher abundances in the low-intertidal zone (12.3 ± 1.8) than in the mid-intertidal zone (0.5 ± 0.1) ($p<0.001$) (Table 2.2, Fig. 2.4c). The two sites in the north-east sector of the Harbour, Gollans Bay east and Gollans Bay west, both had mussel cover of at least twice that of the next highest value of the other sites, as described above. This is reflected by the large spike in mussel cover relative to the other sectors of the Harbour. Within the low-intertidal zone there was a significant difference between both the northern and southern sides ($p<0.001$), and the eastern and western sides of the Harbour ($p<0.001$). There was a significant interaction between the effects of the north / south separation and the east / west separation ($p<0.001$), with much higher cover at the north-eastern sites (73.5 ± 6.6) than the south-eastern sites (9.7 ± 2.4), south-western sites (05.4 ± 1.6), and south-eastern sites (3.2 ± 0.7).

In the low-intertidal zone *Undaria* and mussels were found together in the same plot (50%) much more frequently than they were found either individually (only *Undaria* 27.5%; only mussels 9.5%), or not at all (13%) (Fig. 2.5). This trend was reversed in the mid-intertidal zone where they were in the same plot only 1% of the time. *Undaria* and mussels were present by themselves in 1% and 36% of the plots in the mid-intertidal zone respectively. The largest proportion (62%) of the plots in the mid-intertidal zone had neither *Undaria* or mussels.

I found a significant relationship between the cover of *Undaria* and mussels in the low intertidal zone (Log transformed data: $r^2 = 0.08$, $p<0.001$, Table 2.3, Figure 2.6a). This is in part due to a large number of plots that had high *Undaria* cover but no mussels at all, and vice versa. When comparing average values across reefs, rather than individual sample plots, there was much stronger relationship between *Undaria* and mussel cover ($r^2 = 0.31$, $p=0.008$, Table 2.3, Figure 2.6b).

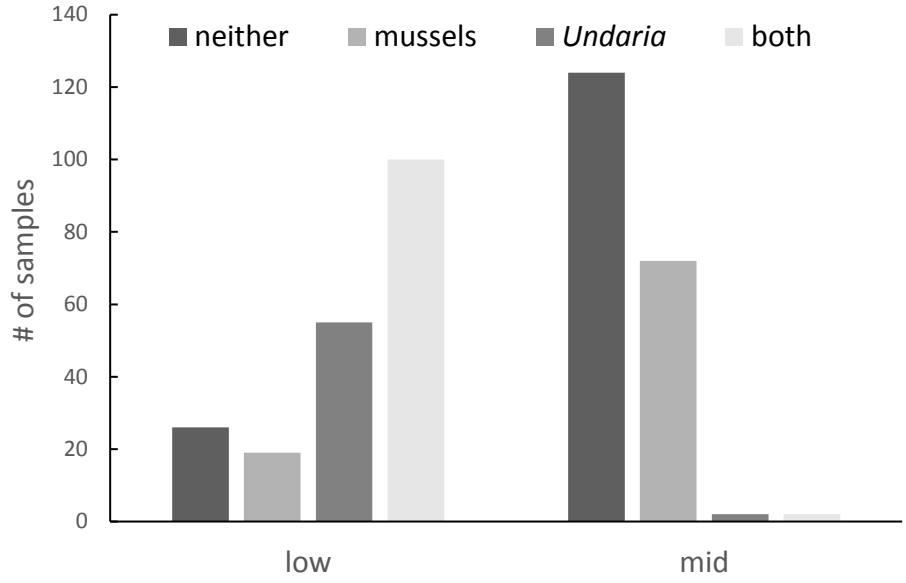

Figure 2.5. Number of survey plots in Lyttelton Harbour where *Undaria* and mussels were found together, by themselves or entirely absent in the low and mid-intertidal zones (n = 400). Bars = 1 SE.

Table 2.3. Linear regression between *Undaria* and mussel cover, log transformed *Undaria* and mussel cover at an individual sample level, and between log transformed reef average *Undaria* and mussel cover, in the low-intertidal zone (n = 10 per reef at 20 reefs). Degrees of freedom: Regression = 1, residual 198. Significant results are highlighted in bold.

Response	**Test factor**	**SS**	**F**	**p**
log *Undaria* × log Mussel	Regression	6.29	16.96	**<0.001**
	Residual	73.45		
	Total	79.75		
log site *Undaria* × log site Mussel	Regression	1.40	8.51	**0.008**
	Residual	3.12		
	Total	4.51		

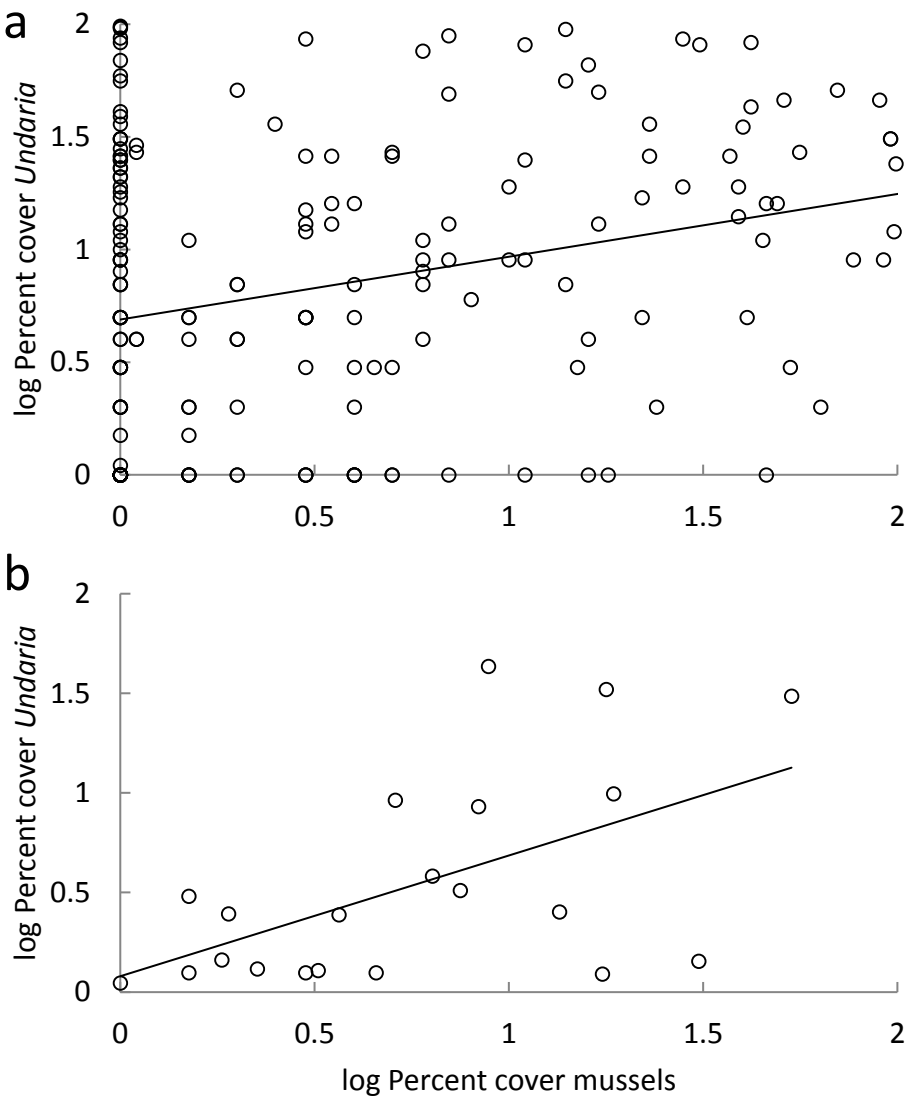

Figure 2.6. Relationships between log transformed *Undaria* and mussel cover (a) at an individual sample level (n = 200), and between log transformed reef average *Undaria* and mussel cover (b), in the low-intertidal zone (n = 10 per reef, 20 reefs).

Pile Bay temporal survey

Undaria varied significantly between sample months ($p < 0.001$, Table 2.4, Fig 2.7a), and there was a significant difference in *Undaria* cover both between photos taken outside and inside of the *Undaria* growing season ($p<0.001$), and photos taken with low and high mussel cover ($p<0.001$, Table 2.5, Fig. 2.7b). *Undaria* cover was the highest in association with mussel beds than without, both inside (22.6 ± 1.0 vs 20.0 ± 0.6) and outside (9.9 ± 1.3 vs 4.9 ± 0.5) of *Undaria*'s expected growing season. Post hoc Wilcoxon analysis showed that all pairs of factors (i.e. outside growing / low mussel vs. inside growing / high mussel) were

significantly different from each other (p<0.001 for all pairs). Mussel cover varied slightly between seasons (p<0.001, Table 2.4, Fig. 2.7c), but did not differ between *Undaria* growing and senescence seasons (p=0.61, Table 2.5, Fig. 2.7d). There was a statistically significant difference between the low mussel and medium-high mussel levels (p<0.001, Table 2.5, Fig. 2.7d), were mussel cover, obviously, was much higher in the mussel beds 'treatment' (25.5 ± 0.7 vs 1.1 ± 0.1), and did not change with the *Undaria* growing season.

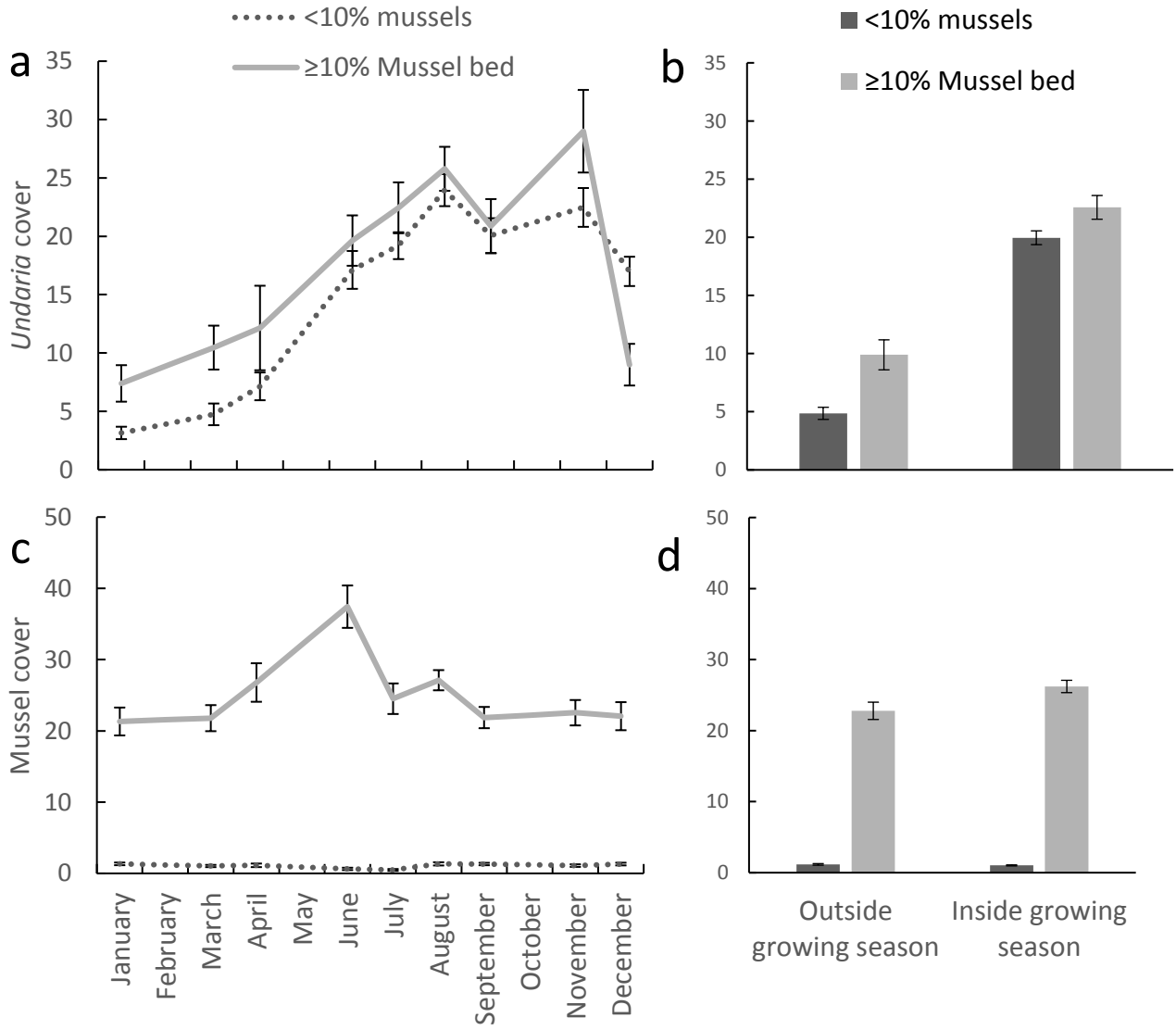

Figure 2.7. Variation in *Undaria* cover between sample months (a) and between the *Undaria* growing season with or without associated mussel beds (b) on Pile Bay reef in Lyttelton Harbour, New Zealand. Variation in total mussel cover between sample months (c) and between the *Undaria* growing season with or without associated mussel beds (d) on Pile Bay reef in Lyttelton Harbour, New Zealand. Bars = 1 SE.

Table 2.4. Kruskal-Wallis test for effect of sample month on the cover of *Undaria* and mussels on Pile Bay reef in Lyttelton Harbour, New Zealand. Degrees of freedom: Month = 8. Significant results are highlighted in bold.

Response	Test Factor	Kruskal-Wallis chi-squared	p
Undaria cover	Month	411.0	**<0.001**
Mussel cover	Month	52.08	**<0.001**

Table 2.5. Wilcoxon signed-rank test for differences in *Undaria* and mussel cover between *Undaria* senescence and growth seasons, and between samples without and with medium-to-large (>10% cover) mussel covers. The table also includes post-hoc analysis for *Undaria* cover. Treatment combinations have been abbreviated as follows: *Undaria* senescence season = S, *Undaria* growth season = G, without mussel bed = 0, with mussel bed = 1. Significant results are highlighted in bold.

Response	Test Factor	W	p
Undaria cover	*Undaria* season	136370	**<0.001**
	Mussel beds	168010	**<0.001**
Mussel cover	*Undaria* season	333470	0.609
	Mussel beds	0	**<0.001**
Undaria cover	S0 × S1	7344	**<0.001**
	S0 × G0	98094	**<0.001**
	S0 × G1	11104	**<0.001**
	S1 x G0	23902	**<0.001**
	S1 × G1	3268	**<0.001**
	G0 × G1	106600	**<0.001**

Undaria attachment survey

Undaria was found attached to three main substrate types; coralline turfs, bare rock and encrusting paints, and mussel shells. The number of *Undaria* individuals attached to each substrate type was very similar between the two headlands sampled (Fig. 2.8). Turf was the most common attachment substrate on both headlands (51% and 46%), followed by bare rock and paint (38% and 41%), and mussels (11% and 13%). However, when comparing between the wave-exposed headlands, and the relatively wave-sheltered coves, the frequency of different attachment substrates did differ (Fig. 2.8). In the coves *Undaria* was attached to turf (57%) more frequently than bare rock or paint (40%), and almost never attached to mussels (3%; in part because there are much fewer mussels here, unpubl. data).

Undaria sampled at the headland were attached to turf (40%) and bare rock or paint (39%) in virtually similar proportions but were also commonly attached to mussels (21%). The chi-square test showed that attachment substrate type was non-independent with wave exposure ($p<0.001$) but independent to site ($p=0.76$, Table 2.6). There was no significant difference in the length of sampled *Undaria* individuals between substrate types or sample site ($p=0.458$, 0.882), but there was a difference between wave exposure levels ($p=0.016$, Table 2.7, Fig. 2.9), with larger individuals on the headlands than coves (68.6 ± 2.4 vs 59.7 ± 2.3). There were no significant interactions between any of the test factors.

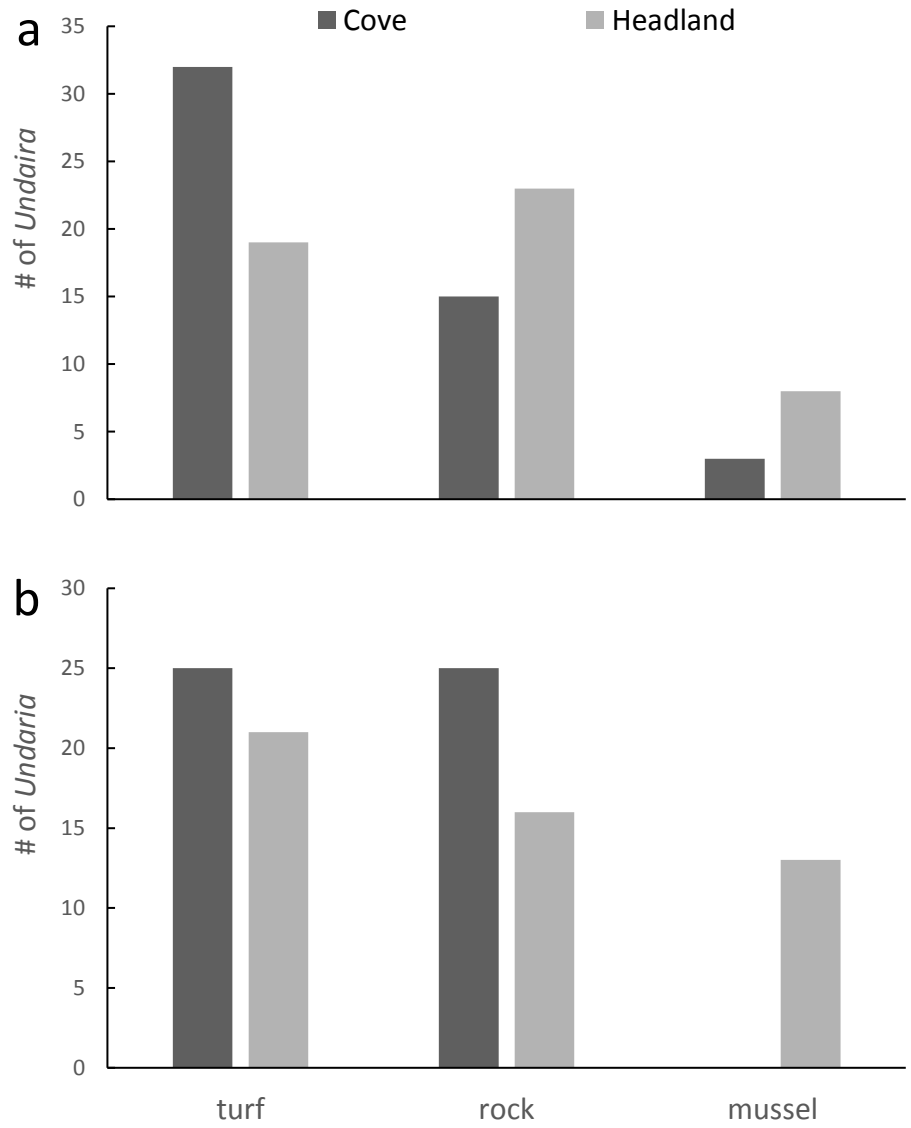

Figure 2.8. Proportion of *Undaria* attached to different substrate types on wave-sheltered coves, and wave-exposed headlands, on two headlands (a & b) at Pile Bay reef. n = 100.

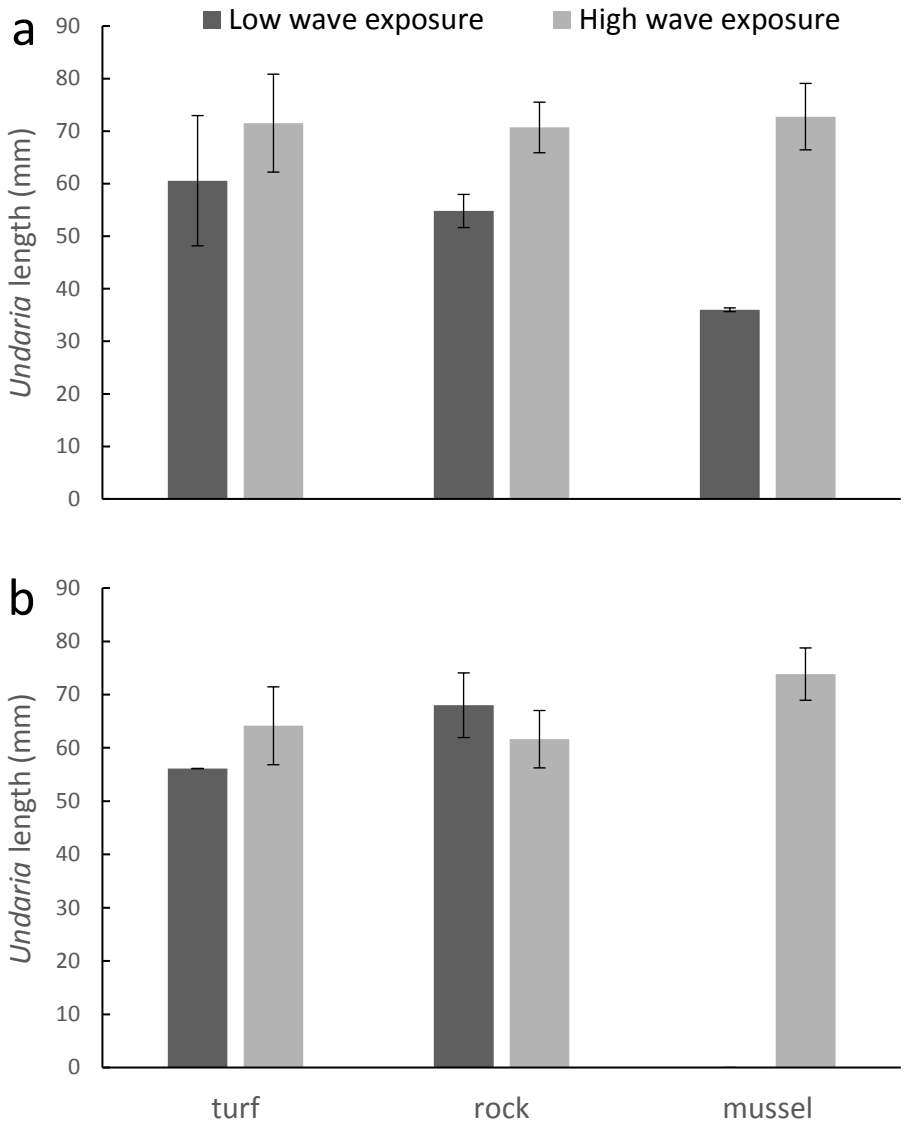

Figure 2.9. Average length of *Undaria* attached to different types of substrate, at different levels of wave exposure, on two sample headlands (a & b) on Pile Bay reef. No Undaria was found attached to mussels at the low wave exposure site (i.e., in coves). n = 100 Bars = 1 SE.

Table 2.6. Chi-squared test of independence between wave exposure level (low in cove, high on headland), sample site (A & B), and *Undaria* attachment substrate type (coralline turf, rock & encrusting algae, mussels). n = 200. Degrees of freedom: Site = 3, Wave exposure = 3. Significant results are highlighted in bold.

Response	**Test Factor**	**Pearson's chi-squared**	**p**
Attachment substrate	Wave exposure	16.49	**<0.001**
	Site	0.54	0.764

Table 2.7. Three-way ANOVA testing for effects of *Undaria* attachment substrate, wave exposure, and sample site, on the length of measured *Undaria* individuals. Degrees of freedom: Attachment substrate = 2, Wave exposure = 1, Site = 1, Attachment substrate x Wave exposure = 2, Attachment substrate x Site = 2, Wave exposure x Site = 1, residual = 189. Significant results are highlighted in bold.

Response	**Test Factor**	**SS**	**F**	**p**
Undaria length	Substrate	880.9	0.78	0.458
	Wave exposure	3283.8	5.85	**0.016**
	Site	12.47	0.02	0.882
	Substrate x Wave exposure	2783.2	2.48	0.086
	Substrate x Site	675.0	0.60	0.549
	Wave exposure x Site	1410.2	2.51	0.115
	Substrate x Wave exposure x Site	972.6	1.73	0.190
	Residuals	106028		

2.4 Discussion

Broad distribution patterns

As hypothesized, *Undaria* was found at all 20 reefs sampled in Lyttelton Harbour. *Undaria* has been present in Lyttelton Harbour for approximately 30 years (Hay 1990), and given the natural spread rate of 1-2 km per year documented for South Canterbury (Russell et al. 2008), aided further by human-assisted spread on the hulls of commercial and recreational vessels, it was clearly able to colonize the entire Harbour. However, *Undaria* was more common in the eastern half of Lyttelton Harbour, which is closer to the Harbour mouth, is more wave-exposed, has more rocky shore, and higher abundances of mussels, than the western half of the Harbour where soft sediment shorelines are more common. *Undaria* appears to prefer wave-exposed sites probably because wave action may lead to greater propagule pressure, increased nutrient supply, reduced risk of desiccation during low tide, less consumer pressure, reduced temperature fluctuations and sediment accumulation, all of which would benefit increased settlement, growth and survival (Hurd 2000).

In its native range *Undaria* grows from the low intertidal zone to a depth of ca. 18 m, being most abundant in the lower intertidal zone to ca. 3-4 m depth (Kim et al. 1998). The upper

reach of *Undaria*'s range is approximately the low water neap tide mark, and populations are not common above this elevation (Forrest and Taylor 2002, South et al. 2016). In this study I also found that *Undaria* was more common in the lower intertidal zone, and almost completely absent from the mid-zone, similar to previous studies. However, I did not investigate the sub-tidal populations. The pattern of *Undaria* distribution in the tidal zone was consistent across all 20 sites sampled. The presence of *Undaria* is restricted vertically largely by desiccation stress (Bollen et al. 2017). In addition, there is also a possibility that the presence of native algae in parts of the intertidal area may compete for settlement sites. For example, the low intertidal zone if often dominated by native algal species such as *Hormosira banksii* and *Cystophora torulosa* (Lilley et al. 2016), although the observational data did not allow an investigation of competition.

Relationships between *Undaria* and mussels

The survey data showed that, in the low-intertidal zone, *Undaria* and mussels were found co-occurring in a particular survey quadrat more frequently than either was found by themselves. Moreover, beyond a simple presence / absence relationship, there were also positive relationships between mussel and *Undaria* cover: a relatively weak relationship at the sample level (across the 200 samples from Lyttelton Harbour) and a stronger relationship at the reef level (when the mean cover value for each of the 20 reefs was analysed). This suggests that the two species share preferences for similar microhabitats, or that one species may be facilitating the other. (James and Shears 2016b) suggested that environmental conditions such as sedimentation and wave exposure at many reef sites may play an important part in this pattern. Similar small-scale trends of *Undaria* and mussel co-occurrences have been reported for artificial mussel lines (James and Shears 2016b). Mussels and *Undaria* were observed at approximately similar levels across the tidal zone. Similar to *Undaria*, mussels are also mainly restricted to the lower tidal level. Desiccation stress in the upper tidal zone and increased feeding time in the lower tidal zone implies that mussels are most abundant in the low intertidal and subtidal zones (Kennedy 1976, Marsden and Weatherhead 1999). The most abundant mussel in the low intertidal zone, *Perna*, occurred where conditions are favourable in terms of wave exposure, occurrence of larvae and substrates for settlement, and food supply (i.e., with suitable seston) (Gardner 2000,

Gardner and Thompson 2001, Fox 2003). Mussels are often found together in dense mussel beds where individuals in the centre of the clumps are more protected from environmental stress and predation. Although the environmental requirements and the natural enemies of mussels and *Undaria* differ, the same fundamental mechanisms that decrease desiccation stress and predation/grazing for mussels in mussel beds are likely to have similar effects on *Undaria* individuals that settle on or in-between mussels and thereby produce positive relationship between the two species.

Possible co-existence mechanisms

The seasonal changes in abundances of *Undaria* found overseas, with large sporophyte size and high cover peaking in winter followed by populations senescing and decreasing cover over summer (Morita et al. 2003), have also been reported in New Zealand in several studies (Hay and Villouta 1993, James and Shears 2012), including some also in Lyttelton Harbour (Schiel and Thompson 2012, Thompson and Schiel 2012, South et al. 2016). However, these studies focused on seasonal patterns of *Undaria* only and did not examine any possible interactions with other habitat-forming species such as mussels. I found that although *Undaria* did decrease in abundance outside of the peak winter season, it did so to a lesser degree when associated with mussels. This suggests that in some situations, *Undaria* is able to remain at relatively high abundance even when cover in nearby areas has decreased due to senescence and the large sporophytes are largely absent. It has been hypothesized that the presence of year-round populations of mature *Undaria* sporophytes is related to more favourable temperature ranges and less extreme seasonal fluctuations in some invaded regions (Thornber et al. 2004, Schaffelke et al. 2005, Russell et al. 2008), compared to its native range where dieback occurs due to high sea temperatures during summer (Morita et al. 2003, James et al. 2015). However, the apparent benefit *Undaria* experiences in the presence of mussels, in terms of reduced senescence during summer, is unlikely to be related to more favourable temperatures where mussels occur (i.e., temperatures do not vary across the Pile Bay reef). Alternatively, the apparent effect of mussels on *Undaria* persistence may be due to both *Undaria* and mussels being more common on headlands and other parts of the reef with relatively high wave energy.

Undaria has previously been shown to succeed in areas with high wave exposure (Castric-Fey et al. 1993, Nanba et al. 2011, Peteiro and Freire 2011, James and Shears 2016b), as the additional wave action may lead to greater propagule pressure, increased nutrient supply, reduced risk of desiccation during low tide, less consumer pressure, reduced temperature fluctuations and sediment accumulation, all of which would benefit increased settlement, growth and survival (Hurd 2000). Conversely, areas with high wave exposure are also likely to cause an increased rate of dislodgement of mature sporophytes. However, because *Undaria* can have multiple cohorts of recruits (Thornber et al. 2004, Thompson and Schiel 2012), and removal of the adult *Undaria* canopy has been shown to trigger the growth of dormant propagules (Thompson and Schiel 2012), potentially by reducing competition for light, the removal of *Undaria* individuals by waves may facilitate further recruitment. The combination of these factors would suggest that a wave exposed reef would have higher turnover of the *Undaria* population, producing several overlapping cohorts and a more seasonally sustained macroscopic canopy presence. Wave action may thereby increase *Undaria* abundances, although it has also been suggested that excessive wave action can prevent *Undaria* from becoming dominant on reefs on the West Coast of the South Island (South et al. 2017).

While it is possible that the patterns of mussel co-occurrence and increased *Undaria* densities outside of peak season may be due to small-scale environmental factors, it is also possible that the mussels are facilitating *Undaria* settlement. As discussed earlier, mussels could facilitate *Undaria* by increasing suitable attachment surface area (Forrest and Blakemore 2006, O'Connor et al. 2006, Pereyra et al. 2017), and decreasing stressors such as grazing and desiccation (Thompson 2004, Pereyra et al. 2017). Furthermore, the mussels could potentially also facilitate *Undaria* growth by providing nutrients through biodeposition (Vinther and Holmer 2008). Increased settlement, for example, would increase the number of *Undaria* cohorts, and through this mechanism may prolong the cover of mature *Undaria*. Detailed studies of population demographics, reproductive phenology and mechanisms of recruitment and persistence are needed to distinguish among these hypotheses.

At the individual *Undaria* scale I also found that *Undaria* are often growing directly on mussels, which is further contributing to their co-occurrence patterns. *Undaria* has been shown to be able to settle on almost any hard substrate, mussels included (Hay 1990,

Forrest and Blakemore 2006, Sliwa et al. 2006). I found that a greater proportion of *Undaria* individuals were attached to mussels on the wave-exposed headlands than in the wave-sheltered coves. In this study I did not determine the relative abundance of substrate types in the survey area. Therefore, this study does not provide any evidence for substrate type preferences by *Undaria*, but it does show that *Undaria* will settle onto mussels when they are present. However, rather than *Undaria* having a preference for mussels as an attachment substrate, it is likely that this pattern is due to the same mechanisms I have discussed above. *Undaria* and mussels both have higher abundances on the more wave-exposed headlands, so the likelihood of an *Undaria* propagule settling on a mussel is increased. Additionally, the environmental conditions within mussel beds may be more suitable for *Undaria* individuals, and the likelihood of them successfully growing to their macroscopic stages could also increase.

In conclusion, I found that at three different surveyed spatial scales, *Undaria* were frequently in association with mussels. *Undaria* is common on reef sections with dense mussel beds, and when in association with these mussels, *Undaria* exhibited much less seasonal variation than has previously been reported. With the observational, mensurative nature of this study it was not possible to determine the exact mechanisms by which this pattern occurs. However, my findings demonstrate that the relationships between invading species and native habitat-forming species may be important and that it is worthwhile to investigate these interactions. More detailed manipulative and mensurative studies are required to identify the potentially complex mechanisms that facilitate these relationships.

3 Effects of the invasive seaweed *Undaria pinnatifida* on condition of the green-lipped mussel *Perna canaliculus* and abundance of mussel epibiota

Abstract

Invasive species are becoming an increasingly significant issue worldwide, but the impacts on invaded ecosystems and specific species have not been quantified for all invasive species. Here I investigate potential impacts of the invasive seaweed *Undaria pinnatifida* on the native habitat-forming mussel *Perna canaliculus*. Mussels with and without attached *U. pinnatifida* were collected from a reef in Lyttelton Harbour, New Zealand, every month for one year. The health of the mussels was measured using a 'condition index', and the algae and invertebrates associated with the mussel were recorded. I found that the condition index of *P. canaliculus* significantly decreased when an *U. pinnatifida* individual was attached. There was no effect of *Undaria* on algae and sessile invertebrates attached to mussels, but mobile invertebrates were significantly more species-rich and abundant in the presence of *U. pinnatifida*. This significant result suggests that *Undaria's* holdfast provides a new habitat for mobile invertebrates, particularly crustaceans and gastropods, where they potentially experience less desiccation and wave stress, less predation but more food. However, more experimental research would be required to determine the exact mechanisms through which *U. pinnatifida* inhibits the mussels it is attached to and how *Undaria* may facilitate mobile invertebrates. My study highlights a topic that has not been investigated in detail, and the findings may have implications for marine aquaculture, particularly mussel-culturing in areas invaded by *Undaria*.

3.1 Introduction

Many seaweed species have become successful invaders (Williams and Smith 2007, Thomsen et al. 2016a). Two seaweeds, *Caulerpa taxifolia* and *Undaria pinnatifida*, are among the 100 worst invasive species (Lowe et al. 2000). Invasive seaweed can cause significant ecological impacts by out-competing native species, changing ecosystem composition, and ecological interactions (Schaffelke et al. 2006, Molnar et al. 2008, Thomsen et al. 2009, Maggi et al. 2015, Thomsen et al. 2016a). Invasive seaweeds may create economic losses as they can interfere with aquaculture systems, decrease export value, and require control (Pimentel et al. 2005). Fouling on commercial vessel hulls and ballast water associated with shipping as well as intentional releases are thought to be the main pathways for introductions of seaweeds (Perez et al. 1984, Molnar et al. 2008, South et al. 2017). Risk assessments and biosecurity strategies have been developed for invasive seaweeds (Williams and West 2000, Wotton et al. 2004, Molnar et al. 2008, Champion et al. 2014). However, it is difficult to contain and control newly introduced species in the open marine environment where currents and waves constantly disperse propagules.

The kelp *Undaria pinnatifida* (Harvey) Suringar (hereafter referred to as *Undaria*) is one of the most successful marine invaders worldwide (Lowe et al. 2000, Epstein and Smale 2017, South et al. 2017). *Undaria* is native to the coastal waters of China, Japan, and the Korean Peninsula, but is now established in South and North America, Europe and Australasia. Its impacts in invaded areas vary between regions, habitats, environmental conditions and response variables. In Argentina, *Undaria* has reduced native seaweed diversity (Casas et al. 2004). On the other hand, another study from Argentina showed that invertebrate abundance and diversity can increase in the presence of *Undaria* due to the provision of additional habitat (Irigoyen et al. 2011). *Undaria* has become established across New Zealand and can be found in almost all of New Zealand's international ports and surroundings (Russell et al. 2008, South et al. 2017). It is found on many exposed rocky reefs low in the intertidal zone (Russell et al. 2008). While extensive research has been performed on the distribution, physiology and growth patterns of *Undaria* in New Zealand (e.g. (Hay and Luckens 1987, Thompson 2004, Chen 2012, Schiel and Thompson 2012), there have been few detailed studies on its impact on native ecosystems. Studies have found little to no evidence of effects on diversity and only a transient impact on the abundance of a few

native inconspicuous seaweeds (Forrest and Taylor 2002, Schiel and Thompson 2012, South et al. 2016, South and Thomsen 2016). The invasion of and effect on rocky reefs have been studied in detail, but no studies have quantified impacts on rocky-reef associated mussels, even though *Undaria* is often abundant on rocky reefs (see chapter 2).

Perna canaliculus and seaweeds

The New Zealand green-lipped mussel, *Perna canaliculus* (Gmelin) 1791 (Bivalvia: Mytilidae, hereafter *Perna*), is an endemic species in New Zealand found in a variety of habitats ranging from rocky reefs to soft sediment shorelines (Powell 1979, Marsden and Weatherhead 1999, Fox 2003). The habitat preferences of *Perna* and *Undaria* overlap to a large extent, particularly in the upper subtidal/ lower intertidal zone, with the algae growing on or around mussel reefs in close association with *Perna*, and in some cases settling directly onto the mussels (see chapter 2) (Buchanan and Babcock 1997, Woods et al. 2012).

Mussels are often host to a wide variety of epibiotic flora and fauna. It is not uncommon to find barnacles (Cirripedia), limpets (Patellidae and other limpets-like gastropods), tube worms (Canalipalpata), and many other sessile animals growing on their surface (Wahl 1989, Woods et al. 2012). Some algal species, such as encrusting coralline algae (e.g., *Lithothamnion* sp. and *Corallina officinalis*) and, less frequently, larger algal species, like *Fucus vesiculosus*, will also settle on to mussels (Albrecht and Reise 1994, Fletcher 2013).

Several studies have quantified interactions between mussels and large canopy-forming seaweeds. For example, it is possible that attached seaweeds can reduce mussel mortality through visual and physical obstruction of predators (Laudien and Wahl 1999). However, attached fucoid seaweeds have also been found to double the mortality of mussels on a rocky shore in Ireland, especially during storm events due to extra hydrological drag (O'Connor et al. 2006). Even if mussels are not torn off the substrate, mussels may, if large algae are attached, increase production of energetically expensive byssal threads (to increase their probability of survival during storms), which probably decreases growth rate (Thieltges and Buschbaum 2007). This hypothesis was supported by Dittman and Robles (1991) who found that overgrown mussels had significantly lower growth and reproductive rates. Nevertheless, they did not examine the underpinning mechanisms behind these

impacts, but suggested that this reduced growth rate (in addition to energetic cost from increased byssal production) may also be due to epibiota obstructing mussel temperature regulation as epibiota also reduce surface reflectance and increase evaporative cooling (Dittman and Robles 1991). Furthermore, epibiotic species could hamper the feeding abilities of their host species in several ways. Fouling species can limit the ability of their hosts to move and position themselves to reach the best feeding conditions (Thieltges 2005). In mussel reefs, especially on soft sediment, reduced mobility from being overgrown may increase the risk of being buried (or partially buried), which would affect their ability to feed. Moreover, if the host and epibionts occupy similar niches they may compete for resources (e.g. Riera et al. 2002), although in that study competition effects were found to be of minor importance. The American slipper limpet *Crepidula fornicate* is a filter-feeder similar to the mussel *Mytilus edulis* on which it is often found attached to. It has even been observed preferentially positioning themselves with their feeding openings close to the mussels siphon (Thieltges 2005), where *Crepidula* may use the current created by the mussel to increase its own filtration. Similarly, barnacle fouling can also reduce growth in mussels (Buschbaum and Saier 2001). However, this is in contrast to an earlier study by Laihonen and Furman (1986) where no effect was found on the host mussels themselves, even though the barnacles living directly on living mussels had increased growth rates compared to those on empty shells. However, epibionts can sometimes also facilitate mussels, for example by reducing predation rates (Laudien and Wahl 1999). Although barnacle fouling had the smallest effect on starfish predation compared to epibiotic hydrozoans or algae, they are one of the most abundant epibionts on *Perna canaliculus* (pers. obs.), so they may be important in their ecosystem as well.

The health of mussels is usually assessed by a 'condition index' (CI). Several different methods have been used to estimate CI. Baird (1958) defined a 'wet volume' condition index as the ratio of 100 $\times$ wet meat volume (ml) over the difference between whole volume and shell volume. Later versions of CI were based on dry and wet meat and shell weights (i.e., the ratio of 100 $\times$ dry meat weight over wet whole mussel weight less shell weight) (e.g., Hickman and Illingworth 1980). Another variation of calculating CI is to use the ratio of 100 $\times$ tissue weight over total mussel weight (after drying with paper towels) (Garen et al. 2004). In a recent study (Lander et al. 2012) calculated the CI as the ratio of 100 $\times$ dry meat weight

over dry shell weight. The use of CI gives the ability to track bivalve growth and health across seasons, particularly helpful for mariculture to evaluate the commercial value of stock (Camacho et al. 1995, Peharda et al. 2007). Condition index varies across life stages, seasons and with the reproductive cycle, and will further fluctuate depending on environmental conditions such as temperature, salinity, and food availability (Lachowicz 2005). For example, as mussels grow, their soft tissue volume increases but the shell weight increases disproportionally more. Therefore, as mussels grow, their CI decreases slightly.

Reproduction requires large amounts of energy for gametogenesis and spawning, and this appears to be reflected in seasonal changes in CI. In a study replicated across several locations in central (Wellington Harbour and Marlborough Sounds) and northern (Northland and Great Barrier Island) New Zealand, CI tended to be highest in spring and summer and lowest in winter (Hickman and Illingworth 1980). However, this pattern was less clear at the central sites, and there was much variability from month to month (Hickman and Illingworth 1980). Additionally, there appear to be considerable differences between locations related to latitude and water temperature. A study by Fox (2003) in the Marlborough Sounds concluded that *Perna* flesh weight is lowest in winter, around the time of year when the proportion of mussels with mature gonads declined, apparently following spawning. However, Hickman and Illingworth (1980) state that spawning of *Perna* may occur throughout the year but with peaks in spring to early summer and autumn, which suggests that there is only a weaker correlation between spawning and a decline in CI. Several environmental factors can affect mussel CI. For example, under high nutrient conditions, abiotic environmental factors (water temperature, salinity) were more closely related to CI than nutrient availability (Hickman et al. 1991). However, a minimum food level was identified, where concentrations below 200 µg carbon per litre resulted in a sharp decline in CI (Hickman et al. 1991).

Despite the importance of green mussels as reef-forming organisms, green mussels being a major export aquaculture product, and the continued expansion of *Undaria* to more mussel reefs and mussel farms, so far no study (neither in New Zealand or abroad) has quantified ecological interactions between *Undaria* and mussels.

Study aims and hypotheses

In this study I quantified, based on seasonal collections of individual mussels with and without attached *Undaria*, the impacts of *Undaria* on (1) *Perna* itself (condition index), (2) sessile epibiota directly attached to mussels, and (3) large mobile invertebrates associated with mussels, at a reef between Pile Bay and Deep Gully Bay, Canterbury, New Zealand (hereafter referred to as Pile Bay).

I hypothesised that

(i) *Undaria* settlement on mussels will decrease *Perna* tissue weight to shell weight ratio (i.e., lowering the mussels condition index), in general and particularly during winter when *Undaria* is most abundant. This is expected because (1) *Undaria* is likely to affect *Perna*'s feeding ability due to a reduction in water flow, (2) *Undaria* attached to *Perna* probably causes additional physical stress from increased impacts of wave action (3) *Undaria* often is larger in winter during its growth peak, and (4) *Undaria* could lead to impaired thermal regulation. Alternatively, the presence of *Undaria* could reduce heat stress in *Perna* during exposure to sun light at low tide (Tsuchiya 1983, Zardi et al. 2016).

(ii) The abundance and diversity of sessile epibionts decrease in the presence of *Undaria* because it pre-empts space for colonization of other sessile epibionts on the mussel substrate, preventing them from settling and potentially smother and shade epibionts already present on the host mussel.

(iii) The abundance and diversity of mobile epibionts is likely to increase in the presence of *Undaria* because of the additional microhabitat and potential food source attached *Undaria* provide (Irigoyen et al. 2011).

3.2 Methods

Study site

This study was undertaken at a rocky intertidal reef between Pile Bay and Deep Gully Bay on the southern side of Lyttelton Harbour, Canterbury, at -43.617993, 172.765748 (Lat/Long)

(Fig. 1.3). Pile Bay consists of a basaltic platform and interspersed boulder fields with medium to large boulders. It is a semi-exposed reef with swells of 0.5-1.2 meters, occasionally larger than this during storm events. Mussels were collected from the intertidal zone from c. 0.0 m to 1.0 m above lowest astronomical tide (LAT), where the reef generally has a base layer of coralline turf (*Corallina officinalis* (L.)), with stands of fucoid and laminarian algae, interspersed dense mussel beds and patches of bare rock. The dominant algal species from the intertidal–subtidal fringe downwards on the reef are the fucoids *Hormosira banksii* ((Turner) Decaisne) and *Carpophyllum maschalocarpum* ((Turner) Grev), and laminarian algae *Ecklonia radiata* (J. Agardh, 1848) and *Macrocystis pyrifera* ((L.) Agardh). Both *Perna* and the blue mussel, *Mytilus galloprovincialis* (Lamarck, 1819), are present on the reef, with a higher abundance of *Perna* at the eastern end of the reef and an increasing abundance of *M. galloprovincialis* toward the western side of the reef.

Mussel sampling

Perna were collected every month from the 18 May 2015 to 15 January 2017, with minor variations due to tidal cycles and weather conditions (e.g., storms or large swells that submerged the study site). This allowed me to sample multiple seasons and reduce the effect of environmental conditions on the conclusions. Mussels were randomly selected from a 200 m reef section. Five mussels of variable sizes were collected with and without attached *Undaria* individuals, making an effort to collect 'pairs' of similarly sized individuals between *Undaria* 'treatments' (± *Undaria*, i.e. if, by random sampling, I collected a 10 cm long mussel without *Undaria*, I would also collect a nearby 10 cm long mussel with *Undaria*). For mussels to qualify as potential +*Undaria* samples, they had to have at least one attached *Undaria* holdfast with a minimum length of 80% of the length of the host mussel. Samples were removed from the reef using a pry bar to ensure they were cleanly removed, causing minimal damage to the samples and reef. Samples were transported back to the laboratory in separate zip-lock bags to prevent cross contamination of associated mobile fauna.

In the laboratory, samples were stored in a -19°C freezer to euthanize mussels and associated epibionts. Mussels were shucked using a knife and rinsed with fresh water over a 5 mm sieve to remove sediment and collect epibionts. The sieve was rinsed into sample jars

with ethanol. After large epibionts were removed, the length, width, and depth of the mussels was measured as per Hickman (1979), using a digital calliper. All mobile epibionts larger than 5 mm were identified to the order level and counted. Attached *Undaria* individuals were also removed so that their length and dry weight could be measured. Mussels and *Undaria* were laid flat on an A4 paper sheet and photographed (before drying) so that the number and surface area of sessile epibionts could be measured from image analysis (Fig. 3.1).

To determine the mussel condition index and dry weight of attached *Undaria*, samples were moved to a drying oven and left for 3 days at a temperature of 55°C or until no water loss could be observed. After drying, mussel shells, mussel meat, and *Undaria* were quickly weighed to prevent moisture absorption from the air. Weights were measured to the nearest 0.001 g. For mussels I calculated the condition index (CI) (and as used by Marsden and Weatherhead 1999, Lander et al. 2012) as:

$$CI = \text{dry meat weight (DMW)} \div \text{dry shell weight (DSW)} \times 100$$

Figure 3.1. Example of photos used to analyse the algae and sessile invertebrates attached to mussels, showing *Perna* with *Undaria* individuals that had been attached to it, as well as other epibionts including *Corallina officinalis* and *Chamaesipho columna*.

Statistical analysis

Sample dates were divided into seasons defined by calendar months (autumn, March-May; winter, June-August; spring, September-November; summer, December-February). I used two-way ANOVA to test for effects on *Undaria* (presence-absence) and season on (a) mussel sizes, (b) CI, (c) percent cover of sessile epibiota and (d) abundances of mobile epibiota. Bartlett tests were performed to check homogeneity of variance between treatments. In addition, I tested if CI was linearly related to mussel length. All data were analysed using the Excel data-analysis tool pack and R version 3.4.3 (RCoreTeam 2017) and RStudio Version 1.1.383 (RStudioTeam 2016).

3.3 Results

Perna is widespread and occurs at a high density in the subtidal and low intertidal zone along the rocky shore and reef at the study site. *Undaria* is also present throughout the site in the low intertidal and subtidal zone but was found to be more patchy than mussels, with some areas that were densely covered and other areas where it was sparse (see Chapter 2 for details). This allowed consistent sampling of *Perna* with and without *Undaria* to examine the effects of *Undaria* presence on the condition index of *Perna* and the associated epibiota.

Mussel sizes

The average size of mussels was, as expected based on my sampling protocol, similar with (106.0 mm) and without (105.2 mm) attached *Undaria* ($p = 0.8$, Fig. 3.2, Table 3.1). Similarly, there was no effect of season ($p = 0.75$) or interaction between *Undaria* and season ($p = 0.53$) on the sizes of the collected mussels.

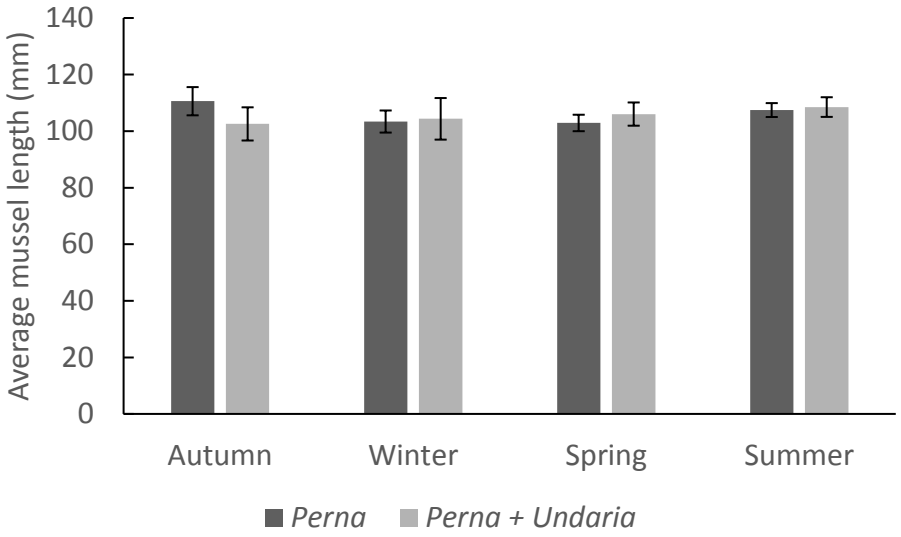

Figure 3.2. Average length of mussels collected for individuals with and without attached *Undaria* in different seasons. (n=10-31). Bars = 1 SE.

Effects of *Undaria* presence on condition index of *Perna canaliculus*

I found a significant effect of both *Undaria* ($p < 0.001$) and season ($p = 0.016$) (but no significant interaction; Table 3.1, Fig. 3.3a) on mussel condition index. The average condition index of mussels, across all sampling dates, was higher without *Undaria* attached (7.62 ± 0.24) compared to mussels with attached *Undaria* (6.22 ± 0.24). *Undaria* caused a reduction in the condition index of 18%. Up until April 2016 there were large monthly fluctuations in CI values (Fig. 3.3b), after which trends became much more consistent. The average seasonal CI across both *Undaria* presence and absence was highest in winter and lowest in spring. There was no large change in CI between summer and autumn.

Overall, a slight negative relationship (-0.027 per additional mm in length) was observed between the length of mussels and their condition index ($p = 0.003$), although there was a lot of variation ($R^2 = 0.049$). This should not have affected the overall conclusions as there was no difference between the average size of mussels collected with and without attached *Undaria* ($p = 0.80$). However, mussels with attached *Undaria* consistently had a reduced CI throughout the size range of mussels (Fig. 3.4) (regression of *Perna* CI and length, $y = -0.034x + 11.28$, $R^2 = 0.054$, $P=0.025$; *Perna* + *Undaria* and length, $y = -0.021x + 8.40$, $R^2 = 0.054$, $P = 0.038$).

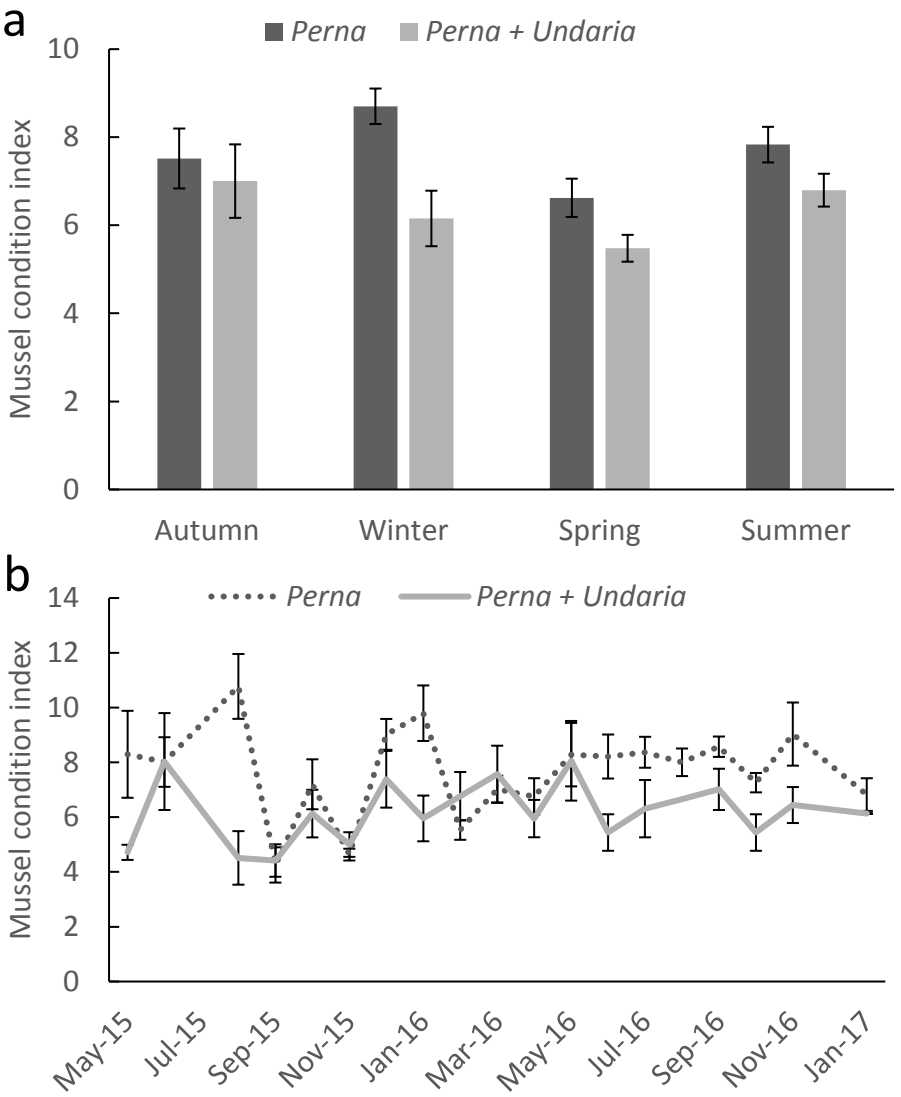

Figure 3.3. Condition index of *Perna canaliculus* with and without attached *Undaria pinnatifida* in different seasons (a, n=10 to 31) and by collection date (b, n=5 per date per treatment). Bars = 1 SE.

Table 3.1. Two-way ANOVA testing for effects of *Undaria* and Season on the length and condition of mussels. Degrees of freedom: *Undaria* = 1, Season = 3, *Undaria* × Season = 3, residual = 170. Significant results are highlighted in bold

Response	**Test factor**	**SS**	**F**	**p**
Mussel length	*Undaria*	25.26	0.07	0.798
	Season	479.3	0.41	0.746
	Undaria × Season	858.8	0.73	0.533
	Residual	66294		
Condition index	*Undaria*	87.07	18.00	**<0.001**
	Season	51.60	3.55	**0.016**
	Undaria × Season	21.24	1.46	0.226
	Residual	822.5		

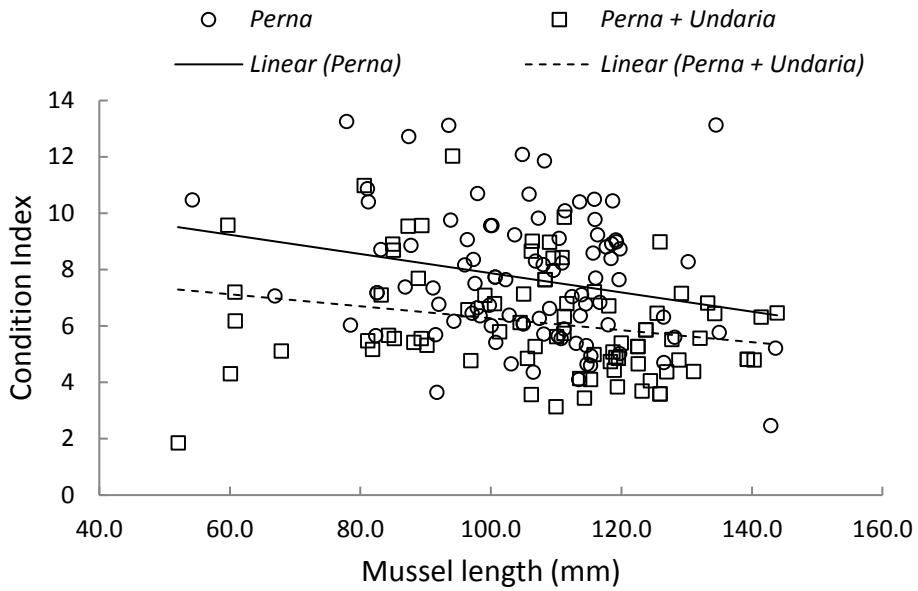

Figure 3.4. Relationship between mussel length and condition index of *Perna canaliculus* with (n=84) and without (n=94) attached *Undaria pinnatifida*. (regression of *Perna* CI and length, y = -0.034x + 11.28, R^2 = 0.054, P=0.025; *Perna* + *Undaria* and length, y = -0.021x + 8.40, R^2 = 0.054, P = 0.038).

Effect of *Undaria* on the abundance of sessile epibiota associated with *Perna*

Mussels were colonized by several species of algae as well as a number of different invertebrate species (Table 3.2). The most common epiphytic algae were coralline turfs, notably *Corallina officinalis*, red encrusting paint (*Lithothamnion sp.*) and the brown alga *Ralfsia* sp. Smaller leafy algae were also recorded in a few samples but were uncommon. Encrusting invertebrates were present in the majority of the samples. *Chamaesipho columna* barnacles were the most frequently recorded, and both *Spirorbis* sp. and *Pomatoceros* sp. tube worms were commonly observed.

Table 3.2. Percent cover and abundance of sessile epibiota associated with *Perna canaliculus* without and with *Undaria* present. (n = 79)

Taxon	***Undaria* absent**	***Undaria* present**
Percent cover		
Coralline turf (*Corallina officinalis*)	52 ± 2.1	72 ± 9.9
Lithothamnion sp.	217 ± 3.3	204 ± 2.6
Ralfsia sp.	47 ± 12.1	245 ± 10.3
Barnacles (*Chamaesipho columna*)	230 ± 14.1	73 ± 4.5
Total	**653** ± 17.7	**701** ± 15.1
Number of individuals		
Spirorbis sp.	53 ± 2.1	70 ± 3.1
Pomatoceros sp.	62 ± 2.3	40 ± 1.4
Total	**120** ± 3.6	**113** ± 3.9

The average species richness of sessile epibiota showed no significant differences between *Undaria* treatments (p = 0.92) (Table 3.3, Fig. 3.5a). Similarly, there was no effect of either *Undaria* or season on percent cover of sessile epibionts combined (Fig. 3.5b, Table 3.3).

The only significant effect of *Undaria* was on *C. officinalis* (p = 0.002) (Table 3.3, Fig. 3.6a), which had lower cover on mussels without than with *Undaria* attached (there was no effects of season and no season × *Undaria* interaction).

Red encrusting *Lithothamnion sp.*, was the most common epiphytic alga on the collected mussels, being found on 47% of the sampled mussels, occurring on 38% of mussels without *Undaria* and 56% of mussels where *Undaria* was present. However, there was no significant effect of *Undaria* (p = 0.40) (Fig. 3.6b) or season (p = 0.19)

There was more variation in the cover of the brown encrusting alga *Ralfsia* than that of red encrusting algae. While red encrusting algae often occurred in smaller patches of ~1% of the total surface area of the mussel, *Ralfsia* commonly occurred in larger patches (>10%) or not at all. Statistically there was no effect of *Undaria* (p = 0.93) (Fig. 3.6c) but cover varied between seasons (p = 0.001), with highest cover in autumn and lowest cover in summer.

Chamaesipho barnacles were overall the most abundant sessile invertebrate recorded, although both *Spirorbis* and *Pomatoceros* tube worms occurred on more individual mussels. They were one of very few invertebrate groups that occurred more frequently on mussels

without *Undaria* than where it was present. Again, there was no effect of *Undaria* (p=0.11, Fig. 3.6d) or season (p = 0.29).

There was no obvious trend in any particular direction for either of the tube worm species observed, both showing large variation both between *Undaria* treatments and season and with no significant effects of either season or *Undaria* (Fig. 3.6e-f, Table 3.3, p = 0.068)

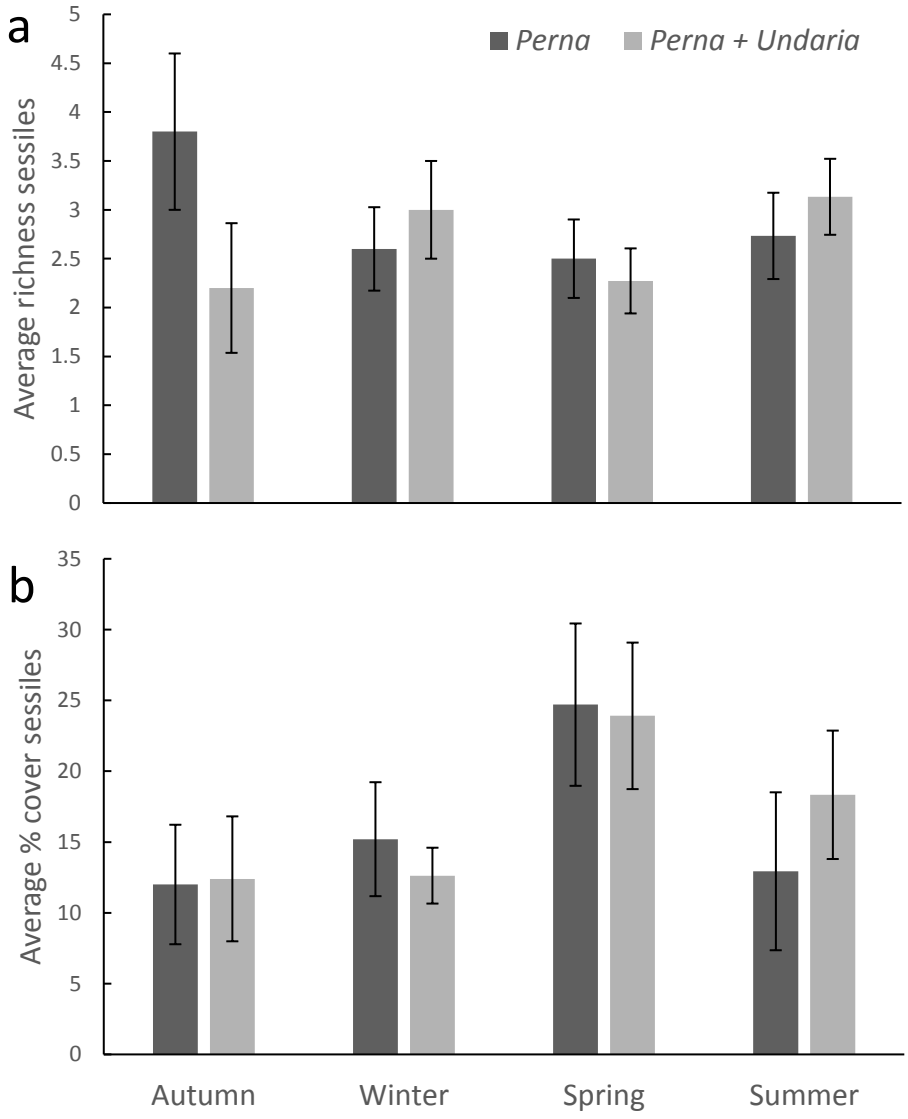

Figure 3.5. Richness of (a) and percent cover (b) of sessile epibiota per mussel associated with *Perna canaliculus* with and without *Undaria pinnatifida* presence across different seasons. (n=5 to 15). Bars = 1 SE.

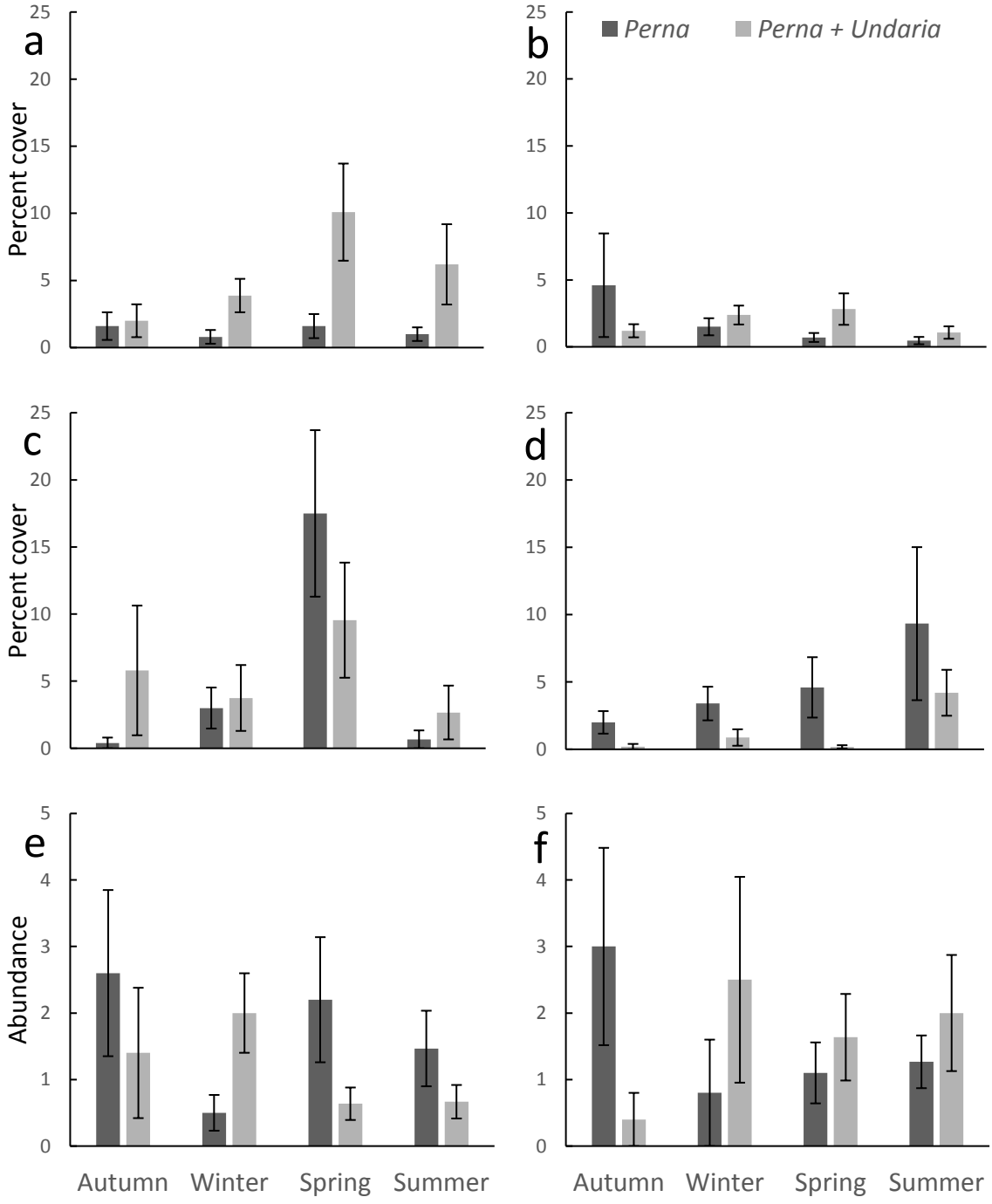

Figure 3.6. Percent cover of *Corallina officinalis* turf (a), *Lithothamnion sp.* (b), *Ralfsia sp.* (c), and *Chamaesipho columna* (d) per mussel associated with *Perna canaliculus* with and without *Undaria pinnatifida* presence across different seasons. Number of *Pomatoceros* (e), and *Spirorbis* (f) tube worms per mussel associated with *Perna canaliculus* with and without *Undaria pinnatifida* presence across different seasons (n=5 to 15). Bars = 1 SE.

Table 3.3. Two-way ANOVA testing for effects of *Undaria* and Season on the sessile community. Degrees of freedom: *Undaria* = 1, Season = 3, *Undaria* × Season = 3, residual = 170. Significant results are highlighted in bold

Response	**Test factor**	**SS**	**F**	**p**
Sessile richness	*Undaria*	0.02	0.01	0.924
	Season	4.49	0.70	0.554
	Undaria × Season	8.57	1.34	0.268
	Residual	151.4		
Sessile abundance	*Undaria*	53.72	0.20	0.657
	Season	1536.1	1.90	0.138
	Undaria × Season	217.7	0.27	0.848
	Residual	19170		
Corallina turf	*Undaria*	515.0	10.14	**0.002**
	Season	168.9	1.11	0.352
	Undaria × Season	133.5	0.88	0.226
	Residual	3607.4		
Lithothamnion sp.	*Undaria*	5.89	0.71	0.402
	Season	40.32	1.17	0.193
	Undaria × Season	52.38	2.10	0.108
	Residual	590.8		
Ralfsia sp.	*Undaria*	0.75	0.01	0.933
	Season	1873.4	5.96	**0.001**
	Undaria × Season	431.9	1.37	0.258
	Residual	7439.4		
Chamaesipho columna	*Undaria*	297.0	2.63	0.109
	Season	433.8	1.28	0.288
	Undaria × Season	32.22	0.10	0.963
	Residual	8025.8		
Pomatoceros sp.	*Undaria*	5.43	1.58	0.213
	Season	7.18	0.70	0.557
	Undaria × Season	25.58	2.48	0.068
	Residual	244.1		
Spirorbis sp.	*Undaria*	4.36	0.62	0.433
	Season	1.13	0.05	0.984
	Undaria × Season	30.83	1.47	0.231
	Residual	497.2		

Effects of *Undaria* on mobile invertebrate abundance associated with *Perna*

The most common invertebrates found on the mussels were isopods (family Sphaeromatidae), limpets (Patellidae), porcelain crabs (*Petrolisthes elongatus* (H. Milne-Edwards, 1837)), and snails (in particular *Austrolittorina sp.*), in that order (Table 3.4). Apart from the limpets, these invertebrates were largely found living within *Undaria* holdfasts (and to a lesser extent on *Undaria* sporophylls). Some other groups that were rarely found included chitons (Polyplacophora), polychaete worms (Canalipalpata) and the pea crab *Pinnotheres novaezelandiae* (Filhol, 1886).

Table 3.4. Abundance of mobile invertebrates associated with *Perna canaliculus* without and with *Undaria* present. (n = 162).

Taxon	***Undaria* absent**	***Undaria* present**
Limpets (Patellidae)	54 ± 1.0	114 ± 0.7
Snails (largely *Austrolittorina sp.*)	1 ± 0.1	45 ± 1.1
Chitons (Polyplacophora)	6 ± 0.3	8 ± 0.3
Sphaeromatidae sp. 1	2 ± 0.2	102 ± 2.3
Sphaeromatidae sp. 2	0 ± 0.0	17 ± 0.6
Porcelain crabs (*Petrolisthes* sp.)	13 ± 0.5	46 ± 1.0
Pea crabs (*Pinnotheres novaezelandiae*)	8 ± 0.3	10 ± 0.3
Juvenile mussels (Mytilidae)	6 ± 0.3	15 ± 0.5
Total mobiles	**90** ± 1.3	**273** ± 3.3

I found significantly higher species richness on mussels with attached *Undaria* ($p<0.001$) and significant differences between seasons ($p = 0.006$) (Table 3.5, Fig. 3.7a), with fewer taxa in winter compared to autumn, spring, and summer. The total number of all mobile invertebrates was also significantly higher on mussels with attached *Undaria* ($p < 0.001$, Fig. 3.7b), but here there was no effect of season (or season × *Undaria* interaction).

Isopods and snails occurred almost exclusively on the mussels with *Undaria* attached, being found in 44 and 30 percent of *Undaria* samples, respectively, compared to 2 and 1 percent in *Undaria* free samples. More specifically, there were no effects of season (or season x *Undaria*) but significantly positive effects of *Undaria* on the abundance of isopods ($p < 0.001$) (Table 3.5, Fig. 3.8a), snails ($p < 0.001$) (Fig. 3.8b), and porcelain crabs ($p<0.001$) (Fig. 3.8c).

The difference for porcelain crabs wasn't as large as that with isopods and snails, occurring in 34% of *Undaria* samples and 11% of *Undaria* free samples.

Finally, unlike the other mobile invertebrates, limpets were not affected by *Undaria* (p = 0.07) (Fig. 3.8d) but abundances varied significantly between seasons (p = 0.01) with higher abundances in spring and summer than fall and winter.

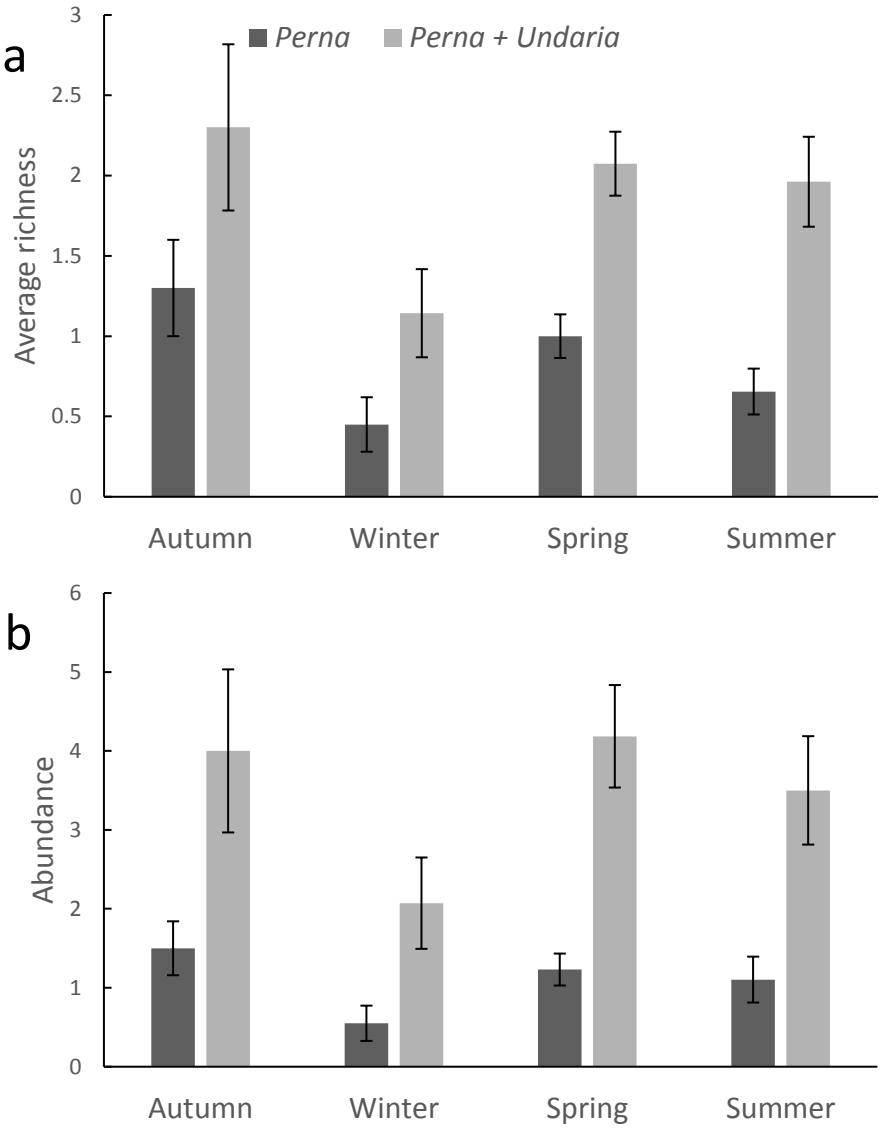

Figure 3.7. Richness (a) and number (b) of mobile invertebrates per mussel associated with *Perna canaliculus* with and without *Undaria pinnatifida* presence across different seasons. (n=10 to 29). Bars = 1 SE

Pea crabs were only found in 9.4% of mussels with, and 13.0% of mussels without *Undaria* but with no significant effect of *Undaria* (p = 0.47), but a significant effect of season (p = 0.034). Pea crabs were most abundant in summer where they occurred in 20% of the mussels collected. They were present in 10% of mussels in autumn and spring, and never occurred in winter. There was no interaction between *Undaria* presence and season (p = 0.519) Additional correlation analysis showed there was no significant relationship between presence of a pea crab in a mussel and mussel condition index (p = 0.893).

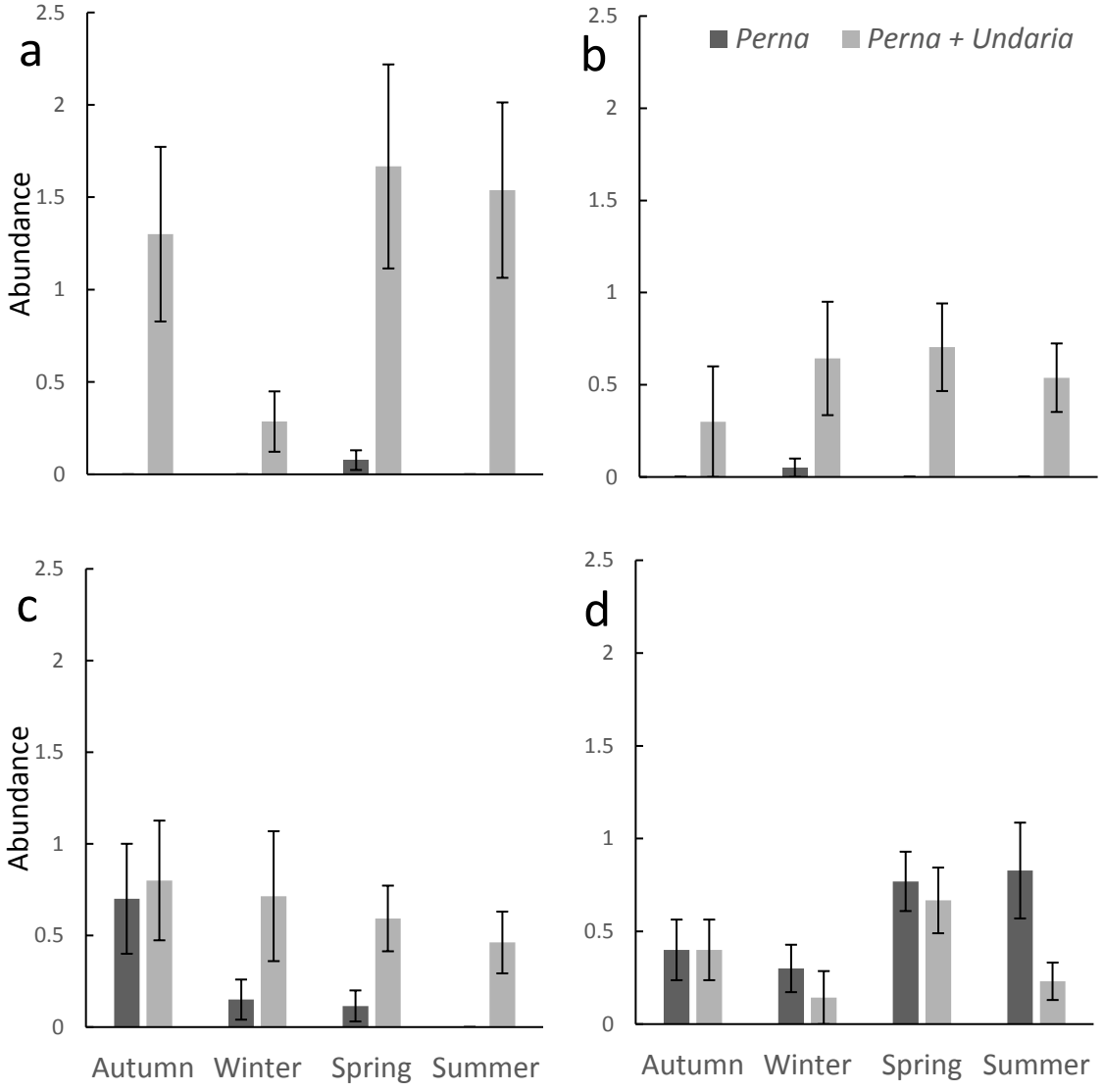

Figure 3.8. Average richness of isopods (a), snails (*Austrolittorina sp.*) (b), porcelain crabs (*Petrolisthes elongatus*) (c) and limpets (Patellidae) (d) per mussel associated with *Perna canaliculus* with and without *Undaria pinnatifida* presence across different seasons. (n=10 to 29). Bars = 1 SE.

Table 3.5. Two-way ANOVA testing for effects of *Undaria* and Season on the mobile community. Degrees of freedom: *Undaria* = 1, Season = 3, *Undaria* × Season = 3, residual = 170. Significant results are highlighted in bold

Response	**Test factor**	**SS**	**F**	**p**
Mobile richness	*Undaria*	49.59	46.05	**<0.001**
	Season	13.75	4.26	**0.006**
	Undaria × Season	1.78	0.55	0.648
	Residual	165.8		
Mobile abundance	*Undaria*	249.81	43.36	**<0.001**
	Season	39.99	2.31	0.078
	Undaria × Season	8.63	0.50	0.683
	Residual	887.2		
Isopods	*Undaria*	68.40	27.32	**<0.001**
	Season	10.22	1.36	0.257
	Undaria × Season	11.08	1.48	0.223
	Residual	385.5		
Snails	*Undaria*	13.25	22.82	**<0.001**
	Season	0.19	0.11	0.955
	Undaria × Season	0.10	0.06	0.981
	Residual	89.40		
Porcelain crabs	*Undaria*	7.98	13.23	**<0.001**
	Season	1.69	0.93	0.426
	Undaria × Season	0.96	0.53	0.664
	Residual	92.89		
Limpets	*Undaria*	2.44	3.33	0.070
	Season	8.41	3.82	**0.011**
	Undaria × Season	0.70	0.32	0.811
	Residual	112.9		
Pea crabs	*Undaria*	0.05	0.54	0.466
	Season	0.86	2.97	**0.034**
	Undaria × Season	0.22	0.76	0.519
	Residual	14.87		

3.4 Discussion

Effects of *Undaria* on condition index of *Perna*

The condition index (CI) of *Perna* changed as hypothesized across seasons, with lowest CI values in spring. Such seasonal changes have been widely observed in *Perna* in New Zealand (Hickman and Illingworth 1980, Fox 2003, Lachowicz 2005), although peaks and lows in CI varied between studies and regions. Differences in CI may be related to mussel size, food availability, water temperature, and spawning. For example, Hickman and Illingworth (1980) noted that CI is inversely correlated with mussel size and water temperature. During winter, phytoplankton levels were found to be low, potentially contributing to a decline in CI during winter in this study (Fox 2003). Spawning typically leads to a drop in CI, and this mainly occurs in spring to early summer and in autumn, although in mussel farms, spawning may occur throughout the year (Hickman 1979, Hickman and Illingworth 1980). Thus, spawning may explain why I found lower CI values in spring. This variability in the time of spawning in *Perna* differs from the more regular spawning timing in other mussels. For example, *Mytilus edulis* in Europe spawns in spring and this also coincides with low CI values (Baird 1966, Okumuş and Stirling 1998). Differences between regions in the time of spawning in *Perna* are likely to contribute to regional variation in CI such as the differences between northern and central New Zealand (Hickman and Illingworth 1980). Unfortunately, most detailed studies on spawning and CI in *Perna* are from other regions in New Zealand. Still, Marsden and Weatherhead (1999) compared CI of *Perna* between shore heights in a number of bays around Banks Peninsula in Canterbury). Interestingly, the CI results of Marsden and Weatherhead (1999) also found a peak in CI in May, followed by a drop in June/July. Condition index was also briefly mentioned in Chandurvelan et al. (2016), but only as before-and-after observations related to the 2011 Christchurch earthquake, so no seasonal or spawning related comparisons were available.

The presence of *Undaria* led to a consistent reduction of the condition index of *Perna* by ca. 20%. This reduction occurred across all seasons but appeared to be greatest in winter, although there was no significant season x *Undaria* interaction. *Undaria* is largest during winter when *Perna* without *Undaria* had the highest mean condition index (Thompson and

Schiel 2012, South and Thomsen 2016, South et al. 2017). Therefore, it could be expected that the impact of *Undaria* on *Perna* is greatest in winter and smallest in summer-autumn when most *Undaria* sporophytes have died back at the end of its typically annual cycle (South et al. 2017). However, in my study the impact of *Undaria* on *Perna* did not differ significantly between seasons (as there was no significant season x *Undaria* interaction). Although *Undaria* has an annual life cycle in its native range, in invaded areas with cooler water, such as most of the South Island shores, this is less pronounced and sporophytes can be found year-round in areas of high water flow (James et al. 2015), with overlapping generations of previous year sporophytes and new recruits (Schiel and Thompson 2012) (see also Chapter 2).

While there are a number of studies on the effects of environmental factors on growth and CI of mussels (e.g. Hickman and Illingworth 1980, Marsden and Weatherhead 1999, Orban et al. 2002, Lander et al. 2012, Chandurvelan et al. 2016), studies examining the effect of biological factors, such as epiphytes, assessed impacts on mussel growth but not CI (Dittman and Robles 1991, de Sá et al. 2007). The effects of *Undaria* on *Perna* condition or growth are similar to those found in other studies examining the effect of macroalgal epiphytes on mussels or other bivalves. For example, the California mussel *Mytilus californianus* had lower growth rates when it was covered with epiphytes of red algae (Dittman and Robles 1991). Likewise, the brown mussel *Perna perna* was significantly smaller in aquaculture when epiphytes (and other fowling organisms) were allowed to grow than when they were removed every month (de Sá et al. 2007). Reduced growth of other bivalves caused by epiphytic algae has been reported by Enright et al. (1983). Conversely, studies in Ireland found that epiphytic algal mats (of *Fucus* and other epiphytic algae) had no effect on mussel growth (O'Connor et al. 2006, O'Connor 2010). In Denmark, Thomsen et al. (2013) found no significant effect of a red alga (*Gracilaria vermiculophylla*) on dry weight of the blue mussel, although the measurements were 'per core', so this may not be particular indicative of mussel growth.

Another potentially important effect of large *Undaria* individuals being attached to mussels is the increased vulnerability to hydrological action, especially on an exposed reef like Pile Bay. Blue mussels, *Mytilus edulis*, have been shown to increase byssal thread production in response to fouling by the American slipper limpet, *C. fornicata* (Thieltges and Buschbaum

2007), and artificial epibiont fouling (Garner and Litvaitis 2017). This is thought to be an energetically expensive process and draws from resources that could have been used for growth or reproduction. As such, this could also contribute to a reduction in mussel CI. Furthermore, epibionts were shown to greatly reduce the rate at which juvenile mussels could move and relocate themselves within a reef, which is important to avoid predators and locate better feeding sites (Garner and Litvaitis 2017). Mussels with large epibionts are also much more likely to be torn off the substrate during storm events. This is supported by a study from Ireland where fucoid epibiota doubled the mortality of mussels on a rocky shore, largely attributed to increased losses during storms (O'Connor et al. 2006). I have recorded lengths of *Undaria* attached to *Perna* of over one meter, at which point these effects are likely to be substantial. However, without tracking individually tagged mussels for an extended period of time, it is difficult to determine how much of a role this plays in the overall reef population dynamics.

Difficulties with comparing condition index between studies

A general problem of comparisons between studies assessing effects on mussel condition index (CI) is that the authors used different ways of defining and calculating CI. Several methods by which CI may be measured have been suggested, which centre around the wet weight, dry weight, or volume of mussels. The different calculations have different strengths and weaknesses, as noted by Hickman and Illingworth (1980). In the following analysis I expand on these findings with my own observations and discuss the different methods.

One of the more popular methods, as used by Fox (2003) and Garen et al. (2004), is based on the wet weight of the mussel tissue. While this is quick and requires no further processing of the mussel, it can be difficult to ensure a similar ‘wetness’ in all samples. This adds unwanted variability in the measured weights and reduces the statistical test power. However, this method has the advantage that it does not damage the mussel tissues, so the mussels may be examined further or used for other studies. The fact that this process leaves the tissue intact and can be performed very quickly means that it is especially useful for quick assays in a commercial setting, and is representative of how the mussel industry processes mussels (Fox 2003). A rough CI value can be rapidly produced on site to estimate

how a mussel crop has been performing during the season and whether it may be ready for harvest.

By drying the samples in an oven or through a freeze-dryer one can remove this variability and then calculate the dry weight CI. This method is the most commonly used (Marsden and Weatherhead 1999, Orban et al. 2002, Lander et al. 2012, Chandurvelan et al. 2016), and was the one I used. Unlike wet weight CI, dry weight CI assessment is more time consuming and requires that samples be taken to the lab, where drying can take up to several days, before data can be analysed.

Shell cavity volume and tissue dry weight have been used to calculate CI in oysters (Medcof and Needler 1941), where shells may be less regular so weights would generate more variation in CI values. However, it is difficult to accurately measure the shell cavity, and this is not necessary with more regular shells such as mussels.

Percent solids (1 – percent water) has been used as a measure of CI by Lachowicz (2005) and Hickman and Illingworth (1980). Curiously, Hickman and Illingworth list what appears to be the same formula twice, only written slightly differently. Specifically, CI weight and percent solids are both described as CI = dry tissue weight x 100 / (wet whole weight – wet shell weight). This may just be a typo rather than an error in the experimental methodology as they have produced different values of results listed in the paper. However, it is not clear what exactly the calculations of Hickman and Illingworth (1980) were because they did not define their variables clearly. The percent solids method has the same vulnerability as the wet weight condition index discussed earlier, that it is difficult to ensure the same 'wetness' between samples. Having compared the different ways of calculating CI, it is clear that the use of the dry weight CI is preferable for detailed scientific studies because it reduces unwanted variability and is more accurate than the other methods of measuring CI.

Effect of *Undaria* on the abundance of sessile epibiota associated with *Perna*

Overall there was very few effects of *Undaria* on sessile epibiota. This may because many of the other algal species commonly found on mussels are much slower growing than *Undaria* and as such were likely present before the *Undaria* settled and would survive for 5-8 month corresponding to the life span of an *Undaria* holdfast. The only species affected was

Corallina officinalis which was more abundant in the presence of *Undaria*. Mussel shells have uniform and smooth surfaces that are potentially difficult for *Undaria* spores to settle on. The complex structure of *C. officinalis* probably offers a much more suitable substrate for *Undaria* juveniles. This notion is supported in other studies that have shown high recruitment of *Undaria* on red algal turf substrate (Schiel and Thompson 2012, Thompson and Schiel 2012, South et al. 2016, South and Thomsen 2016). Thus, the statistical effect is likely more caused by a positive effect of *Corallina* on *Undaria* than of Undaria on *Corallina* the other way around.

Undaria does not appear to have any impact in any particular direction on the number of *Pomatoceros* and *Spirorbis* tube worms attached to *Perna*. The tube worms may simply be so small and sparse that the holdfasts of *Undaria* individuals attached to *Perna* are simply too small to have any impact on the area available for epibiotic worms. Alternatively, tube worms could be equally present on mussels and *Undaria* shows no preference toward mussels with or without tube worms present.

Overall, there is relatively little evidence that *Undaria* affects colonisation or development of sessile epibionts on mussels (perhaps, excluding barnacles), and that instead some epibionts affect settlement of *Undaria* juvenile. Consequently, it would not be expected that indirect effects of *Undaria* via sessile epibionts affect mussels or mussel condition. However, if this was the case, then several potential mechanisms could lead to effects of epiphytes on mussels. These could include reduced growth of mussels overgrown by epiphytes either through obstruction of temperature regulation or reduced ability of filter feeding as suggested by Dittman and Robles (1991), or conversely, increased survival of mussels due to protection from predators as shown by Laudien and Wahl (1999).

Effects of *Undaria* on the abundance of mobile invertebrates associated with *Perna*

Overall, I found more taxa and number of mobile invertebrates in the presence of Undaria across seasons. There are two main mechanisms through which the presence of *Undaria* likely made the immediate environmental conditions more suitable for invertebrates. First, the *Undaria* holdfast and sporophyll provide shelter for smaller invertebrates, and many can take refuge there during low tide. Isopods and snails were the most abundant invertebrates

within the holdfast (but a few polychaete worms were also occasionally observed there). The second mechanism through which *Undaria* increases invertebrate abundance is by acting as an additional food source. Grazers were much more common, overall, on mussels with *Undaria* attached. Snails and boring isopods were almost exclusively present on mussels which were hosting an *Undaria* individual. These results support many other 'seaweed epibiota' studies that typically find high numbers of mobile crustaceans and gastropods inhabiting with seaweeds (Anderson et al. 1997, Thiel and Vásquez 2000, Tuya et al. 2011).

An *Undaria* individual can have a surface area many times larger than that of a mussel to which it is attached, so it would be expected that this is reflected in an increase in invertebrates occupying this habitat. Therefore, *Undaria* should increase the abundance and possibly also the species richness of invertebrates present solely due to the virtue of it increasing the available surface area, before any other mechanisms have an effect. In addition, the complex holdfast of *Undaria* with root-like branches and the physically complex reproductive structure may both provide invertebrates with shelter from predators and exposure to the sun during low tide. For example, I often observed in the field that isopods sheltered in the holdfast on mussels with *Undaria*.

Relatively high abundance and richness of invertebrates associated with invasive *Undaria* and other invasive seaweeds have been described by others (Schmidt and Scheibling 2006, Suárez Jiménez 2015, Arnold et al. 2016). In New Zealand, *Undaria* had similar numbers of associated invertebrates when compared to native macroalgal species with comparably simple physical structures (*Marginariella urvilliana* and *Xiphophora gladiate*), but fewer associated invertebrates than other, more complex macroalgal species (*Carpophyllum flexuosum*, *Cystophora scalaris*, *Sargassum sinclairii*) (Suárez Jiménez 2015). In Nova Scotia, the invasive *Codium fragile* supported a more diverse epifauna than native *Laminaria* species (Schmidt and Scheibling 2006). In England, epibionts associated with *Undaria* were less diverse than those of native perennial kelp species but similar to assemblages with macroalgae with a shorter seasonal life history like *Undaria* (Arnold et al. 2016). Therefore, *Undaria* may have a negative impact on invertebrate abundance in rocky reefs with predominantly morphologically complex macroalgal species, especially if any replacement of these occurred. Conversely, it would have a significant positive effect on mussel reefs where it can fill gaps in the macroalgal canopy, or where no macroalgae were present. The

immediate vicinity around a mussel would potentially see a large increase in mobile invertebrate abundance if an *Undaria* individual settled on it.

Many native grazers feed on *Undaria* in New Zealand. For example, the cat's eye snail, *Lunella smaragda*, has been observed grazing on *Undaria* (Sinner et al. 2000) and native New Zealand grazers were found to feed on *Undaria* just as frequently as on other native macroalgal species (Suárez Jiménez et al. 2015). The gastropods Cooks turban (*Cookia sulcata*) and paua (*Haliotis iris*), one of the main grazers on New Zealand rocky reefs, did not show preference toward any specific macroalgal species and fed on *Undaria* just as much as the other species available (Suárez Jiménez et al. 2015). An exception to the other grazers was the isopod *Batedotea elongate*, which barely consumed any *Undaria* (Suárez Jiménez et al. 2015). In other countries, several different groups of animals have been recorded grazing on *Undaria*, most commonly sea urchins and gastropods (Teso et al. 2009) although crabs and fish have also been recorded feeding on *Undaria* (Thornber et al. 2004). Grazing by the northern kelp crab, *Pugettia productus*, among other grazers, was shown to prevent almost a whole cohort of *Undaria* individuals from reaching reproductive maturity in California (Thornber et al. 2004). This suggests that even though some grazers may be negatively affected, the presence of *Undaria* may well increase the overall productivity of a reef. In New Zealand, most grazers appear to benefit from the food source provided by *Undaria*. It has comparable nutritional value and toughness to some native New Zealand macroalgal species, without any apparent feeding deterrents, suggesting that it would be an ideal target for grazing (Suárez Jiménez 2015). While I did find a huge increase in the number of snails on mussels with attached *Undaria*, it is unclear whether the gastropods are feeding on the *Undaria* itself or on the secondary algal biofilms that grow on its surface.

It is difficult to determine whether any of the mobile invertebrates associated with *Undaria* affected mussels or mussel condition negatively. Potential effects of associated invertebrates include increased predation and parasitism of mussels and interference with feeding or respiration. However, compared with the direct effects of *Undaria* on mussels (see above), the effects of associated invertebrates are likely to be small or negligible, except perhaps the effect of pea crabs which are parasitic on mussels (Bierbaum and Ferson 1986). Pea crabs were found in a similar number of mussels with and without *Undaria* attached, although they were very rare in the mussels that I collected so, at least in my study, their

effects were probably minimal. It is unlikely that the presence of *Undaria* has any effect on how attractive a given mussel individual is to a pea crab looking for a host, but the presence of *Undaria* could possibly provide shelter for pea crabs outside of mussels.

In *Mytilus edulis*, pea crabs have been shown to steal food strands and damage the host mussel gills while doing so (Bierbaum and Ferson 1986). Under high nutrient conditions pea crabs did not affect mussel growth (measured by changes in shell length), but under low nutrient conditions infested mussels showed shell shape distortions indicative of reduced growth rates. Contrary to what Bierbaum and Ferson (1986) found, in my study there was no significant difference in the condition index between mussels with and without pea crabs. However, as stated above, pea crabs only occurred in a very small proportion of the collected mussels, making it difficult to identify small potential effect sizes. Additionally, my experimental design means that it is impossible to tell how long a pea crab has been living inside a mussel and to which extent a mussel's growth may have been impaired.

Perspectives, future studies and conclusions

There have been many studies that examined the effect of *Undaria* on other macroalgal species native to the regions it invades, and several on whether it has any impact on associated invertebrates. But no studies that I am aware of have examined whether *Undaria* affect mussels. My study showed that *Undaria* can have a negative impact on host species such as *Perna* as indicated by a reduced condition index. A reduction in condition index means that mussel individuals may be less able to withstand poor environmental conditions and may not be able to allocate as much resources toward reproduction. This is on top of the increased risk of being ripped off from the substrate during storm events.

Most sessile epibiotic species occupy only a fraction of the mussel's shell surface (typically < 10% cover, see Fig. 3.6), perhaps explaining why I found no effects of the seaweed on sessile epibiota. A larger spatial survey collecting more mussels from more sites would be helpful to re-examine interactions between *Undaria* and sessile epibiota in more detail.

Nevertheless, while I only collected mussels from a single reef, my results generally support past studies. Furthermore, my results also highlight that *Undaria* – mussel interactions on mussel aquaculture lines should be studied, to test if this invasive species have negative

impact on mussel production, mussel taste, and sale values. It would also be interesting to repeat this study but with native macroalgal species, to determine whether the negative effect on host mussel condition index varies between algal species.

Although I documented negative impact on mussel condition, my study does not determine the exact underpinning mechanisms. Further studies, under more controlled laboratory setting, focusing on specific physiological mussel traits, such as reproductive tissue weight, filtration rates, absorption rates, stress-proteins and respiration rates, might help to identify the mechanisms through which *Undaria* produces the trends observed.

I also found that *Undaria* facilitated mobile invertebrates, that appeared to be in particular associated with the holdfasts (Anderson et al. 1997, Thiel and Vásquez 2000, Tuya et al. 2011) rather than the mussel itself. This implies that facilitation would occur whether the *Undaria* was attached to a mussel or simply to the substrate, and also that these organisms have to find other habitat when the holdfast senescence (it typically lives for less than a year). Additionally, because the sampling was performed at low tide, it was not possible to determine whether the invertebrates collected are also associated with *Undaria* when they were submerged during high tide or simply gathering there for shelter once the water subsides. Whether the increased number of invertebrates in general or any particular invertebrates have any effect on the mussels was not directly examined in this study. It is possible that any of several direct or indirect effects of *Undaria* could be responsible for mussel condition, and without any targeted experiments studying the effects of associated invertebrates, it is difficult to determine how and how much any invertebrates had an effect.

In this study I found that *Undaria* can have negative impacts on the condition index of mussels it is attached to. Although *Undaria* did not affect the sessile community associated with mussels, it greatly facilitated the mobile invertebrate community species richness and abundance.

4 Effects of Undaria and mussel removals on Undaria recruitment and algal and invertebrate community composition

Abstract

Invasive species continue to expand their ranges as a result of modern shipping and transport systems. These species encroach into the habitats of naturally occurring species, where they potentially change local community structures and functions. Here I investigated the interactions between the invasive kelp *Undaria pinnatifida* and the native New Zealand habitat-forming mussel *Perna canaliculus*, and their effects on the associated algal and invertebrate community. Both *U. pinnatifida* and *P. canaliculus* were removed monthly over a period of one year from 0.25 x 0.25 m plots in a factorial experiment. Algae and both mobile and sessile invertebrates were quantified after 10, 15 and 25 months. I found that more *U. pinnatifida* recruited into plots with *P. canaliculus* than without. Community composition was only slightly affected by *U. pinnatifida* presence, but *P. canaliculus* had a more marked effect, especially on the invertebrate community and on canopy-forming algal species. Furthermore, an unprecedented hot summer appeared to reduce the cover of all reef species at the final sampling date, after which *U. pinnatifida* colonized plots where native algal species had dominated prior to the hot summer. Even though *U. pinnatifida* had only limited impacts on the reef community, this study demonstrates that native species can facilitate the invasion of alien species. The effects of the hot summer also highlight that future warming may make native ecosystems more vulnerable to invading species.

4.1 Introduction

Invasive species continue to expand their ranges aided through modern shipping and transport systems (Williams and Smith 2007, Hulme 2009, Keller et al. 2011). This is an especially important problem in the marine environment because it is more difficult to prevent the arrival of new species (than in the terrestrial environment), and more difficult to successfully remove and eradicate them once they have become established. Global

warming is also increasing the ability of invasive species to spread, as the region of suitable temperature and other environmental conditions shifts (Stachowicz et al. 2002, Occhipinti-Ambrogi 2007) and native communities are increasingly stressed (and therefore, perhaps, less resistant to invasions). By settling into new areas, invasive species encroach into the habitats of naturally occurring species, where they have the potential to greatly change local community structures and functions (Clavero and Garcia-Berthou 2005, Didham et al. 2005, Molnar et al. 2008, Thomsen et al. 2009). Invasive species can achieve this through a variety of direct and indirect effects, for example by directly competing with native species for limiting resources or by making the habitat less suitable for native species (e.g., by smothering the benthos), and can also facilitate the establishment of more invasive species (Bax et al. 2003, Grosholz 2005, Kluza et al. 2006, Simberloff 2006, Katsanevakis et al. 2014). This is of interest to local governments, as invasive species can make areas less suitable for public use, and can damage economically important systems such as fisheries and aquaculture (Kluza et al. 2006, Katsanevakis et al. 2014).

Undaria pinnatifida (Harvey) Suringar (hereafter referred to as *Undaria*) is one such invasive species which has been listed as an important invader worldwide (Lowe et al. 2000, Silva et al. 2002, Casas et al. 2004, Epstein and Smale 2017, South et al. 2017). In New Zealand *Undaria* was first recorded in 1987 (Hay and Luckens 1987) but can now be found in almost all of New Zealand's international ports and several other ports and surrounding coastal habitats from Rangaunu in the north to Stewart Island and Snares Islands in the south (Russell et al. 2008, Chen 2012, South et al. 2017). *Undaria* has limited success invading established macroalgal communities, but is able to quickly recruit into gaps in native canopy cover (Forrest and Taylor 2002, Valentine and Johnson 2003, Schiel and Thompson 2012, Thompson and Schiel 2012, South et al. 2016). In addition, *Undaria* is an efficient invader of aquaculture facilities, in particular on mussel lines (Woods et al. 2012) and has been observed invading natural mussel reefs (see Chapter 2-3). There have been several experimental studies that, through removal experiments, have tested how *Undaria* affects native plant and animal communities (Casas et al. 2004, Valentine and Johnson 2005, Irigoyen et al. 2011, South et al. 2016, South and Thomsen 2016). Importantly, these studies have all tested for impacts on native communities, such as seaweed, sessile and mobile

invertebrates or fish, on algal covered rocky reefs. By contrast, I am not aware of any manipulative removal experiments from other habitats such as mussel dominated reefs.

Mussels and other bivalves are important ecosystem engineers, that increase habitat complexity and make habitats more suitable for other species (Gutiérrez et al. 2003, Borthagaray and Carranza 2007, Buschbaum et al. 2009, Bateman and Bishop 2017). For example, a meta-analysis by Bateman and Bishop (2017), found that overall, the presence of bivalves led to an increase in both species density and species abundance of associated invertebrates. However, in this analysis the effect of mussels was more context dependent than that of other bivalve groups such as oysters and pinnids, perhaps because they create a slightly more homogeneous habitat compared to oyster reefs or large pinnid shells, or because impact data exist for a variety of different mussel-dominated habitats, including mudflats, sedimentary estuaries and rocky reefs. This review also highlighted that, according to their review, very few research papers have tested, with manipulative experiments, for impact of mussels on rocky shore organisms (Bertness et al. 2004, Silliman et al. 2011, Lemieux and Cusson 2014).

In a mussel removal experiment (20% removed three times over four weeks), plots without mussels had different community structures and lower richness, but similar abundances, of sessile invertebrates, compared to plots with mussels (Valdivia and Thiel 2006). Furthermore, removal treatments had no effect on mobile or semi-sessile invertebrates or either the richness or abundance of algal species. Species with low mobility and poor abilities to cling to the substratum where most affected by mussel removal (Valdivia and Thiel 2006). Where mussels are disturbed, some algal species, such as the small kelp *Postelsia palmaeformis*, recruit onto bare rocky space into areas where mussels have been removed (Paine 1979). Another intertidal study found that, although mussels feed on algal spores, there was still higher abundance of some algal species under live mussels in the intertidal zone, compared to empty shells or no mussel cover, probably because desiccation stress was reduced in this microhabitat (Santelices and Martinez 1988). A study in Uruguay found significantly higher richness of (particularly sessile) invertebrate species in areas with high mussel cover compared to areas without mussels (Borthagaray and Carranza 2007). There was also a positive relationship between the abundance of mussels and the abundance of invertebrates within mussel patches. Finally, in Patagonia, Argentina, mussels

facilitated an entire invertebrate community resulting in 20 times higher diversity in areas where mussels were present compared to neighbouring bare rock (Silliman et al. 2011). With the exception of limpets and barnacles, invertebrates were found almost exclusively associated with mussels. Contrary to these studies, Lemieux and Cusson (2014), found no difference, on artificial created assemblages of mussels and fucoid seaweed, on the total abundance or diversity of the associated species between different assemblages of habitat-forming species.

Given that only few studies have tested for impact of *Undaria* and mussels on local communities, and that no studies have tested for interaction effect between these two species, I carried out a factorial experiment testing for impact of both species on algae and invertebrate communities.

I hypothesised that

(i) Mussels, in particular the native green lipped mussel, *Perna canaliculus* (hereafter *Perna*), increase the rate of *Undaria* recruitment as it facilitates the settlement of *Undaria* spores and protects juveniles from grazing and desiccation.

(ii) The algal and invertebrate communities in plots where *Undaria* and *Perna* are present differ from plots where *Undaria* and *Perna* have been removed, due to both taxa acting as ecosystem engineers probably increasing available attachment area, reducing predation pressure, environmental stress (in particular desiccation), and potentially also providing a food source.

4.2 Methods and materials

Study site

Effects of *Undaria* and *Perna* were studied an intertidal rocky reef between Pile Bay and Deep Gully Bay on the southern side of Lyttelton Harbour, Canterbury, at -43.617993, 172.765748 (Lat/Long) (Fig. 1.3). The experiment was set up along a 200 m section of coast, consisting of a basaltic platform and interspersed boulder fields with medium to large

boulders. It is a semi-exposed reef with swells of 0.5-1.2 meters, occasionally larger than this during storm events. The study was performed in the intertidal zone (approximately 0.3 m lowest astronomical tide), where the reef generally has a base layer of coralline turf (*Corallina officinalis* (L.)), with stands of fucoid and laminarian algae, interspersed dense mussel beds and patches of bare rock. The dominant algal species from the intertidal–subtidal fringe downwards on the reef are the fucoids *Hormosira banksii* ((Turner) Decaisne) and *Carpophyllum maschalocarpum* ((Turner) Grev), and laminarian algae *Ecklonia radiata* (J. Agardh) and *Macrocystis pyrifera* ((L.) Agardh). Southern bull kelps, *Durvillaea poha* (C.I. Fraser, H.G. Spencer & J.M. Waters) and *D. antarctica* ((Chamisso) Hariot) are common on the boulder fields between heads. *Perna*, the blue mussel (*M. edulis* (L.)) and ribbed mussel (*Aulacomya maoriana* (Iredale)) are present on this reef, with higher abundance of *Perna.* All my plots were set up in areas dominated by *Perna*.

Experimental design and sampling

Experimental quadrats were initially set up and treatments applied on the 25th of December 2015. Twenty quadrats of 25 x 25 cm, separated by >2m, with high densities of both mussels and *Undaria*, and similar elevation levels (Fig. 4.1) were marked with corner cow-tags (drilled in with anchor screws), and allocated at random to the following treatments (i) *Undaria* removal, (ii) Mussel removal, (iii) *Undaria* and mussel removal, and (iv) a control (no removal). Three mussel species were found on the reef (*Perna canaliculus*, *Mytilus galloprovincialis*, and *Aulacomya maoriana*) and all were removed from mussel removal quadrats. Mussels and *Undaria* were removed using a pry bar, or by pulling them off by hand. In the *Undaria* only removal treatment, *Undaria* individuals that were attached to mussels were detached from the host mussel. To ensure that *Undaria* and mussels from outside the quadrats did not affect treatments, borders were cleared around all removal plots; mussels were removed from an additional 10 cm around each plot and *Undaria* was removed such that no frond could reach within 10 cm of the quadrat. Mussels and *Undaria* removed from each quadrat were collected in plastic zip lock bags for later laboratory processing.

Figure 4.1. Control removal plot with dense cover of both *Undaria* and *Perna*.

After the initial quadrat clearing, the experimental treatments were maintained every month, from the 25th of December 2015, to the 16th of November 2016. Exact monthly dates varied slightly to accommodate tidal and weather conditions as access to the quadrats was difficult or impossible during spring tides and rough seas. Any new *Undaria* or *Perna* that had recruited into the 'removal treatments' were removed and collected in plastic zip lock bags. As with the initial clearing, borders were also maintained around the quadrats.

All macro-invertebrates and algae (larger than ca. 0.5 cm) in the plots were quantified on 1/10 2016, 1/3 2017 and 25/1 2018, measuring percent cover of sessile species and counting mobile species. Note that the plots were not maintained between March 2017 and January 2018. This did not affect the mussel treatments (because there was no recruitment in this period) – but may have made the *Undaria* removal treatment less efficient (but there are generally few *Undaria* in March). Attached *Undaria* individuals were also removed so that their length and dry weight could be measured. The dry weight of removed *Undaria*, was measured after 3 days of drying at 55°C.

Statistical analysis

All data were collated in Excel and analysed using R version 3.4.3 (RCoreTeam 2017), RStudio Version 1.1.383 (RStudioTeam 2016), and PRIMER-E and PERMANOVA+ (Clarke and Gorley 2006, Anderson et al. 2008). First, I compared dry weight and number of new *Undaria* recruits in the *Undaria* removal plots only, with or without mussels, using a one-way ANOVA (pooling plot data for the whole sample period). Second, I tested for effect on *Undaria* and mussel cover, total algal and canopy cover, algal taxa and invertebrate taxa richness, with two-way ANOVA, for the October 2016, March 2017 and January 2018 sampling dates, separately. I analysed the sample dates separately as the data was temporally non-independent and therefore violates test assumptions. Additionally, warmer sea temperatures changed the community structure making comparisons across all dates inappropriate. Homogeneity of variance was confirmed using the Bartlett test. Finally, I tested for effects on multivariate community structures (again for each of the three sampling dates) with 2-way Permanova (based on Bray Curtis similarity metrics and 4999 permutation). Data was here square root transformed to downplay the importance of the most dominant species. SIMPER analysis followed Permanova to determine the species driving the changes in overall community composition and PCO plots were created to show results graphically.

4.3 Results

Undaria and *Perna* removal and recolonisation

More *Undaria* recruited into (and was then removed) from the plots where mussels were present (Fig. 4.2, Table 4.1). The dry weight of *Undaria* that was removed from plots with mussels was significantly greater than those where mussels had also been removed ($p=0.006$, 11.2 ± 5.5 compared to 1.88 ± 1.3 per 0.0625 m^2). The number of *Undaria* individuals removed also appeared to be greater but this was marginally non-significant ($p=0.064$, 32.0 ± 16.4 compared to 12.6 ± 11.8 per 0.0625 $m^{2)}$. The dry weight spike in May was due to one plot where 13 g dry weight of *Undaria* was removed. November had several plots with larger amounts of *Undaria* removed.

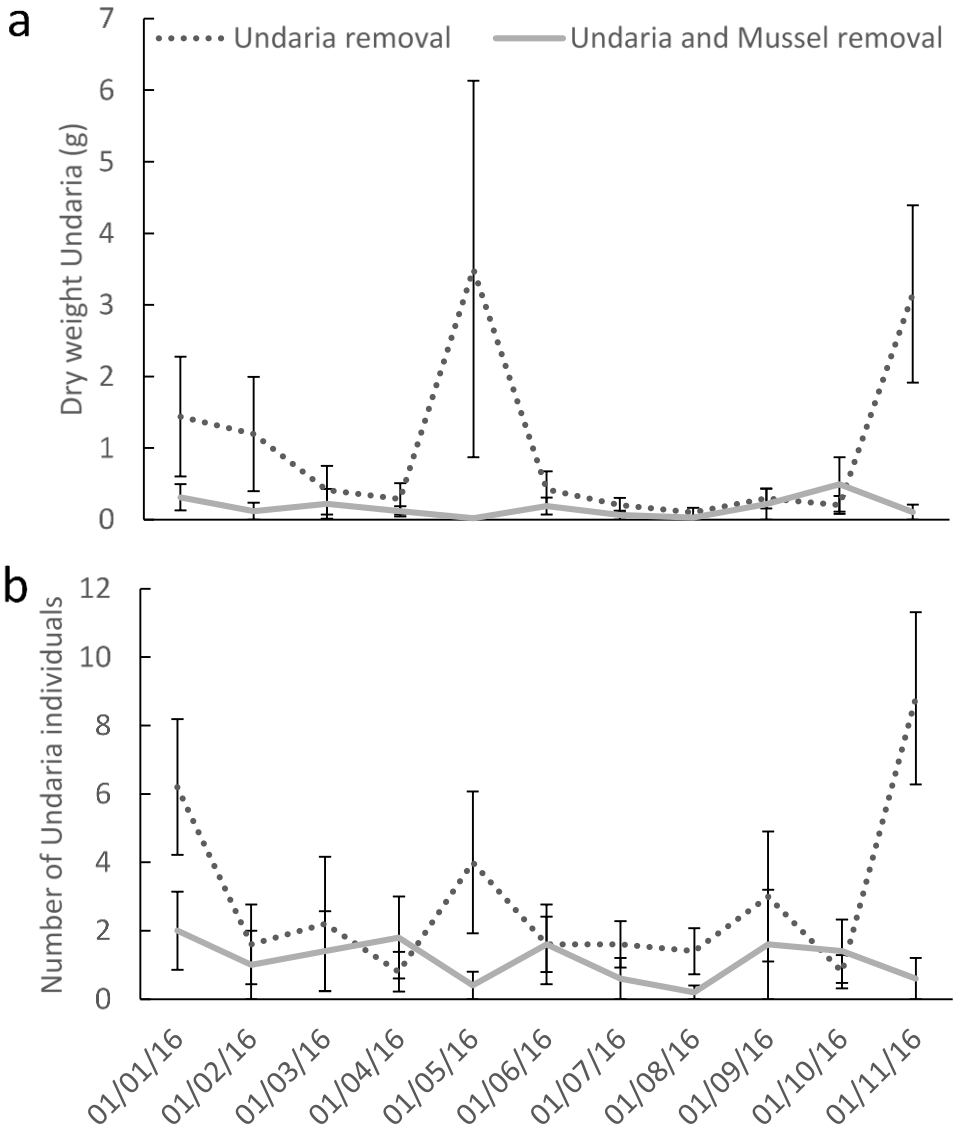

Figure 4.2. Average dry weight (a) and number (b) of *Undaria* removed from experimental plots where either only *Undaria*, or both mussels and *Undaria* were removed every month for one year. (n= 5 per treatment per 11 sample dates). Bars = 1 SE.

Table 4.1. One-way ANOVA testing for effects of mussel removal on the dry weight and number of *Undaria* that had recruited into *Undaria* removal plots over the course of the experiment. Degrees of freedom: Mussels = 1, residual = 8. Significant results are highlighted in bold

Response	**Test factor**	**SS**	**F**	**p**
Undaria dry weight	Mussels	217.8	13.76	**0.006**
	Residual	126.7		
Undaria number	Mussels	940.9	4.59	0.064
	Residual	1639.2		

Perna canaliculus was the dominant mussel and accounted for approximately 92% of mussel cover in plots, with *M. galloprovincialis* and *A. maoriana* making up approximately 5% and 3% of cover, respectively. Over the course of the entire experiment, no mussels, visible to the naked eye, recruited into any plots after the initial removal treatment.

Percent cover and richness of algal and invertebrate species occurring in plots

The first community sampling was performed in October 2016, one month before the last removal treatment. A second survey was carried out five months later, in March 2017, and a third and final survey in January 2018. The third survey revealed a substantially reduced cover of *Undaria* (see below), which was most probably due to mortality caused by unusually warm sea surface temperatures in the summer of 2017-18 (see discussion, below). Due to the potential impact of this 'heatwave' on community structure, it was inappropriate to compare treatment effects over time, so each survey date was analysed separately.

In total 33 different algal taxa, and 51 invertebrate taxa were identified in the 20 plots and 3 sampling dates. Excluding the target species *Undaria*, the most commonly occurring algal taxa were *Dictyota* spp., *Halopteris* spp., *Carpohyllum maschalocarpum*, and *Corallina officinalis* (Table 4.2). The invertebrate taxa that were observed in the most plots were *Cantharidella tesselata*, *Chamaesipho columna*, *Sypharochiton pelliserpentis*, and *Austrominius modestus* (Table 4.2).

Undaria cover was, as expected, lower in plots where this species was experimentally removed, although there was only a significant difference during the first sample date ($p=0.005$) and a near significant difference on the second sample date ($p=0.057$) (Fig. 4.3, Table 4.3). During the last sample date there was no significant difference in *Undaria* cover ($p=0.127$) (Fig. 4.3); however, at this sample date there was an unusually low *Undaria* cover across all treatments, including the control (no removal). Mussel removal had no significant effect on *Undaria* cover during any of the three sample dates ($p=0.577$, 0.206, and 0.234 respectively) (Fig. 4.3, Table 4.3) and there was no significant interaction between *Undaria* and mussel removal treatments on *Undaria* cover.

Table 4.2. The most commonly occurring algal and invertebrate species, excluding the experimentally manipulated species, *Undaria pinnatifida* and the three mussel species, *Perna canaliculus*, *Mytilus galloprovincialis*, and *Aulacomya maoriana*.

Taxa	**Higher classification**	**Percent of samples where taxa present**
Algae		
Dictyota spp.	Dictyoteae	93.2
Halopteris spp.	Sphacelariales	88.1
Carpophyllum maschalocarpum	Fucales	84.7
Corallina officinalis	Corallinales	81.4
Colpomenia sinuosa/peregrina	Scytosiphonales	79.7
Encrusting algae	Corallinales	76.3
Non-geniculate coralline algae	Corallinales	62.7
Ralfsia verrucosa	Ectocarpales	54.2
Invertebrates		
Cantharidella tesselata	Trochoidea	57.6
Lunella smaragdus	Trochoidea	54.2
Chamaesipho columna	Cirripedia	54.2
Cryptosula pallasiana	Gymnolaemata	47.5
Sypharochiton pelliserpentis	Polyplacophora	47.5
Austrominius modestus	Cirripedia	45.8
Cellana radians	Patellogastropoda	44.1
Notoacmea parviconoidea	Patellogastropoda	33.9

Mussel cover did not recover after the initial removal treatment and remained below 5% even more than one year after the last removal treatment was performed (Fig. 4.3). There was therefore, and as expected, much higher cover in the control plots compared to the removal treatments at all three community surveys ($p=<0.001$, <0.001, and 0.005 respectively) (Fig. 4.3, Table 4.3). *Undaria* removal had no significant effect on mussel cover in any of the surveys ($p=0.85$, 0.41, 0.640) (Fig. 4.3) and there was no significant interaction effect between mussel and *Undaria* removal.

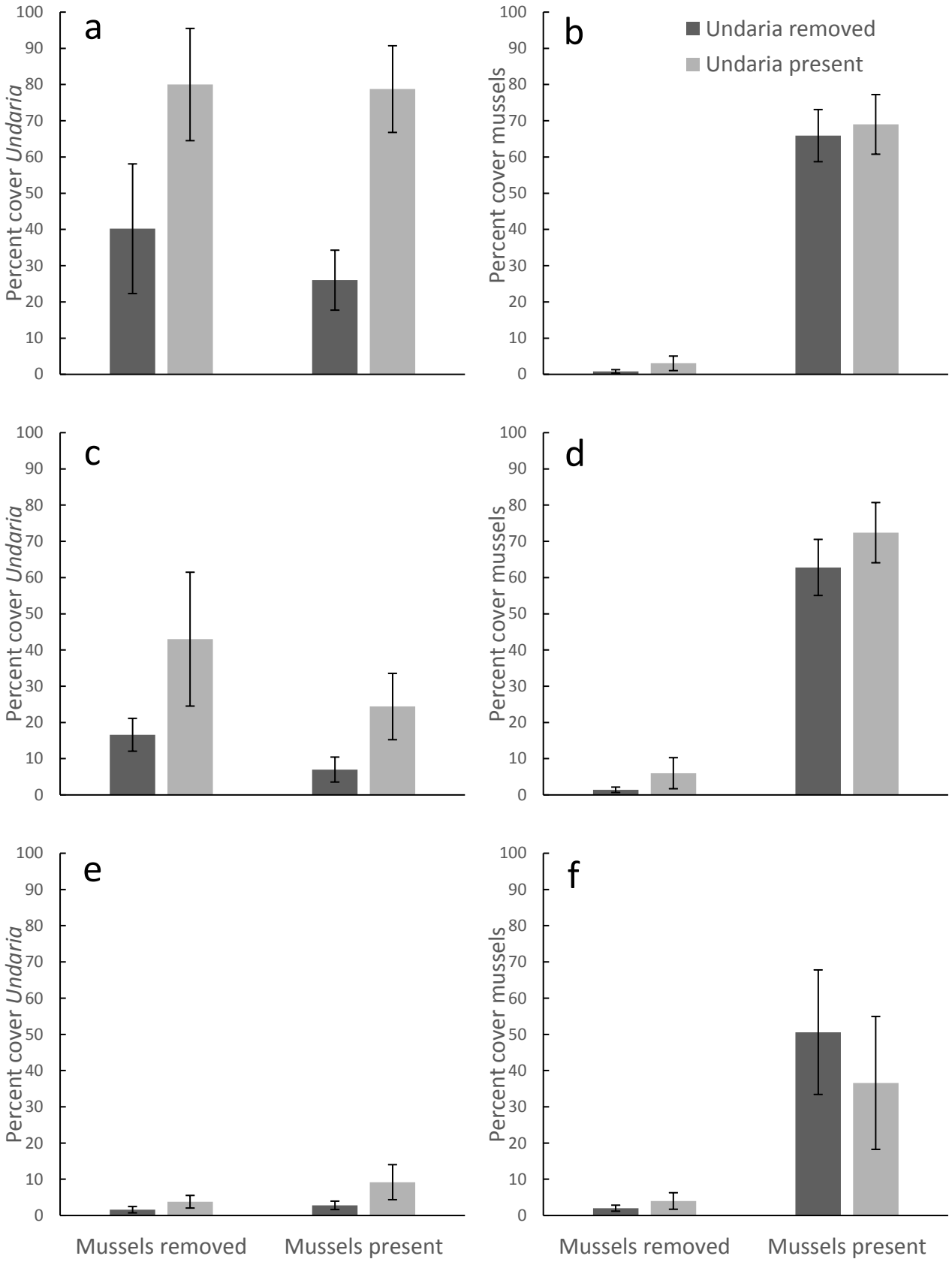

Figure 4.3. Percent cover of *Undaria* and mussels in plots with different *Undaria* and mussel removal treatments on three sample dates; 1/10/16 (a, b), 1/3/17 (c, d), and 25/1/18 (e, f). Bars = 1 SE.

Table 4.3. Two-way ANOVA testing for effects of *Undaria* and mussel removal on the cover of *Undaria* and mussels. Degrees of freedom: *Undaria* = 1, mussels = 1, Undaria × Season = 1, residual = 16. Significant results are highlighted in bold

Response	Test factor	SS	F	p
Undaria cover 1/10/16	*Undaria*	10173	10.68	**0.005**
	Mussel	310.3	0.33	0.576
	Undaria × Mussel	197.3	0.21	0.655
	Residual	14293		
Undaria cover 1/03/17	*Undaria*	2398.1	4.19	0.057
	Mussel	994.1	1.74	0.206
	Undaria × Mussel	101.3	0.18	0.680
	Residual	9152.4		
Undaria cover 1/10/16	*Undaria*	10173	10.68	**0.005**
	Mussel	310.3	0.33	0.577
	Undaria × Mussel	197.3	0.21	0.656
	Residual	14293		
Mussel cover 1/03/17	*Undaria*	4.68	0.036	0.851
	Mussel	20300	157.0	**<0.001**
	Undaria × Mussel	0.87	0.007	0.936
	Residual	1930.0		
Mussel cover 25/01/18	*Undaria*	119.6	0.72	0.407
	Mussel	21839	132.25	**<0.001**
	Undaria × Mussel	110.9	0.67	0.424
	Residual	2642.1		
Mussel cover 25/01/18	*Undaria*	180.6	0.23	0.641
	Mussel	8237.7	10.33	**0.005**
	Undaria × Mussel	319.2	0.40	0.536
	Residual	12760		

Average algal species richness, (excluding *Undaria*'s own taxonomic identity, (Thomsen et al. 2016b)), did not vary much across removal treatments and sample dates, remaining at an average between 7 and 11 species also after the very hot summer of 2017/18 (Fig. 4.4). There was a significant difference in algal richness between *Undaria* removal treatments during the first community survey (p=0.001), with average richness being slightly higher in plots where *Undaria* had been removed (Fig. 4.4). There was no significant difference between *Undaria* removal treatments in either of the other two sample dates (p=0.37, and 0.31) (Fig. 4.5, Table 4.4). Mussel removal treatments had no significant effect on algal richness either (p=0.43, 0.24, and 0.27) (Fig. 4.4, Table 4.4).

No significant difference in invertebrate richness (excluding mussels) was recorded between *Undaria* removal treatments in any of the community surveys (p=0.14, 0.43, and 0.86) (Fig. 4.4, Table 4.4). During the initial and second community surveys, invertebrate richness was significantly higher in plots where mussels were present (p=0.006, <0.001), but this was not the case for the final community survey (p=0.37) (Fig. 4.4).

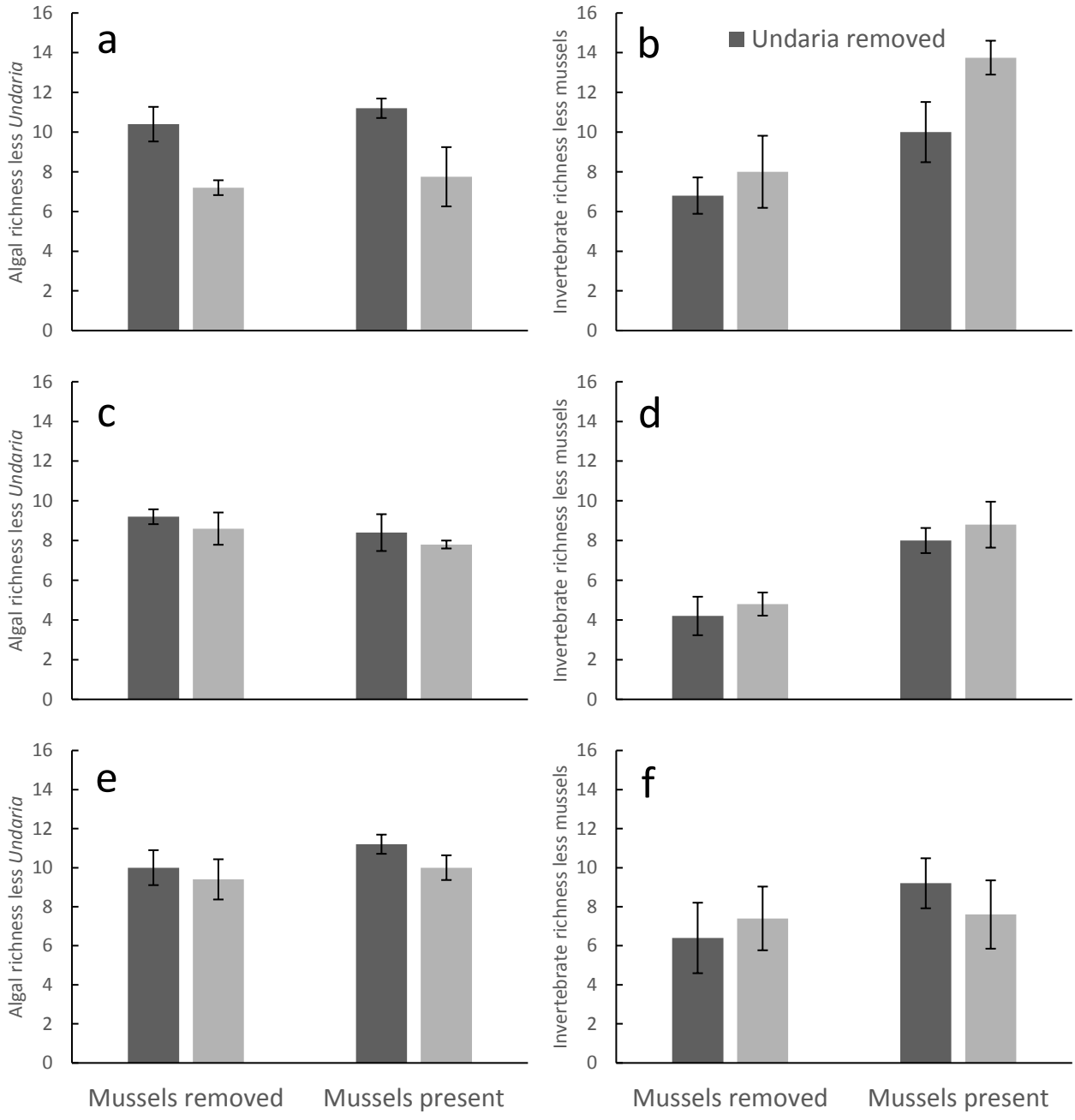

Figure 4.4. Species richness of algae and invertebrate taxa (excluding *Undaria* and mussels) in plots with different *Undaria* and mussel removal treatments on three sample dates; 1/10/16 (a, b), 1/3/17 (c, d), and 25/1/18 (e, f). Bars = 1 SE.

Table 4.4. Two-way ANOVA testing for effects of *Undaria* and mussel removal on the richness of algal and invertebrate taxa (excluding *Undaria* and mussels). Degrees of freedom: *Undaria* = 1, mussels = 1, Undaria × Season = 1, residual = 16. Significant results are highlighted in bold

Response	Test factor	SS	F	p
Algal taxa richness 1/10/16	*Undaria*	53.34	16.15	**0.001**
	Mussel	2.20	0.67	0.427
	Undaria × Mussel	0.074	0.022	0.883
	Residual	49.55		
Algal taxa richness 1/03/17	*Undaria*	1.80	0.85	0.371
	Mussel	3.20	1.51	0.238
	Undaria × Mussel	<0.001	<0.001	1.00
	Residual	34.00		
Algal taxa richness 1/10/16	*Undaria*	4.05	1.30	0.272
	Mussel	4.05	1.30	0.272
	Undaria × Mussel	0.45	0.14	0.709
	Residual	50.0		
Invertebrate taxa richness 1/03/17	*Undaria*	22.01	2.40	0.142
	Mussel	91.42	9.97	**0.007**
	Undaria × Mussel	7.65	0.83	0.375
	Residual	137.6		
Invertebrate taxa richness 25/01/18	*Undaria*	2.45	0.65	0.432
	Mussel	76.05	20.15	**<0.001**
	Undaria × Mussel	0.05	0.013	0.910
	Residual	60.40		
Invertebrate taxa richness 25/01/18	*Undaria*	0.45	0.034	0.856
	Mussel	11.25	0.85	0.371
	Undaria × Mussel	8.45	0.64	0.437
	Residual	212.4		

Average algal cover, excluding *Undaria*, was not significantly different between *Undaria* removal treatments (p=0.11, 0.85, and 0.64) or mussel removal treatments (p=0.068, 0.064, and 0.63), although mussel removal had a near significant effect during the first and second surveys (Fig. 4.5, Table 4.5). Total algal cover had decreased after the 2017/18 summer heatwave with the largest decrease observed in plots where mussels had been removed (Fig. 4.5). There was no significant interaction between *Undaria* and mussel treatments in algal richness or cover in any of the surveys.

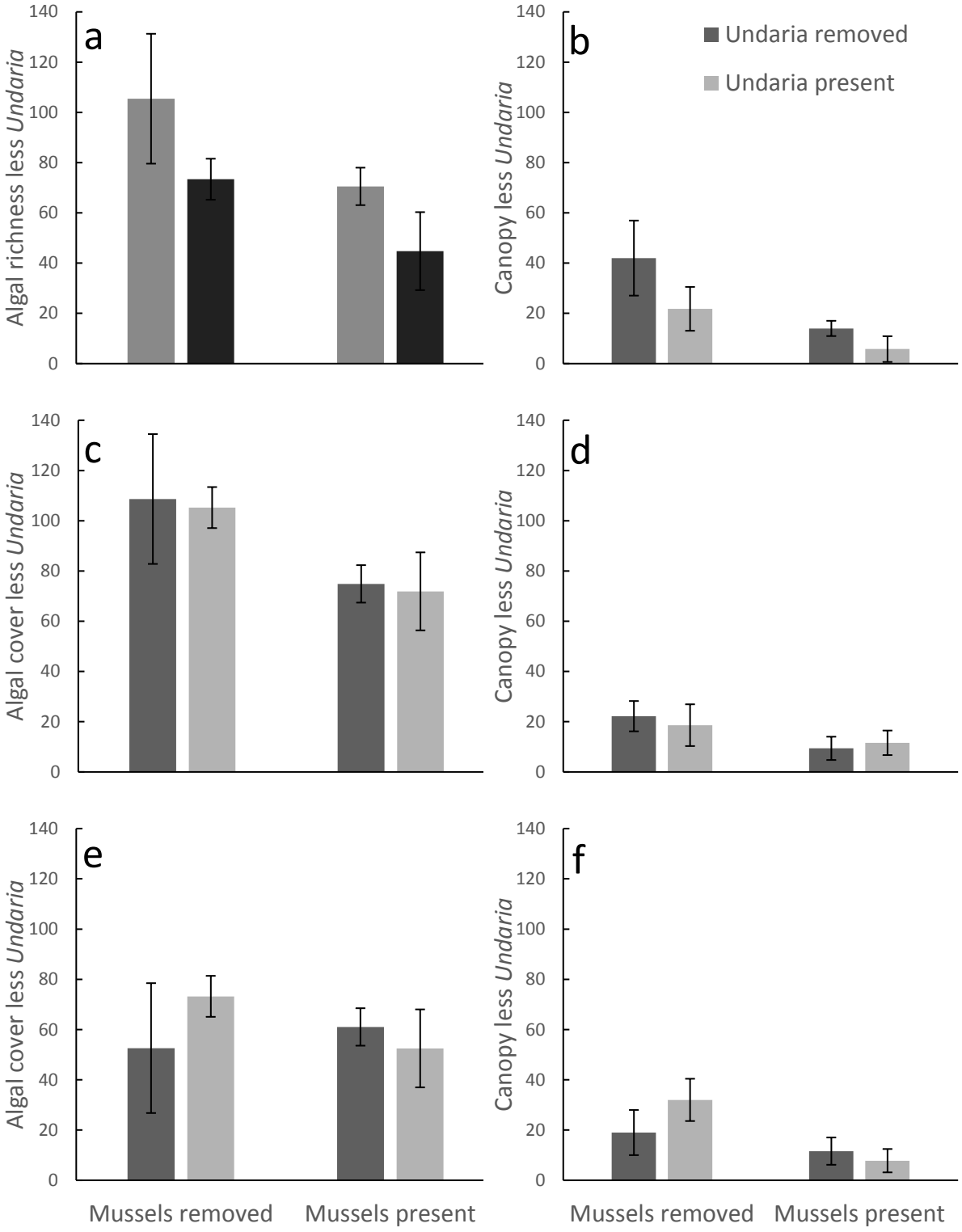

Figure 4.5. Combined percent cover of algae and canopy-forming macroalgal species (excluding *Undaria*) in plots with different *Undaria* and mussel removal treatments on three sample dates; 1/10/16 (a), 1/3/17 (b), and 25/1/18 (c). Bars = 1 SE.

In addition to analysing total algal cover, I grouped all the Fucoid and Laminarian species as canopy-forming species, given they have ecological roles similar to *Undaria*. Although the average canopy cover, excluding *Undaria*, appeared to be higher in plots where *Undaria* had been removed than where it had not during the initial community survey (Fig. 4.5, Table 4.5), this was not statistically significantly so (p=0.18). *Undaria* treatment had no significant effect in either direction in the second and final community surveys (p=0.91, and 0.53). Canopy cover was significantly lower in plots where mussels were present during the first and final community surveys (p=0.034, and 0.041), but not significant in the second survey (p=0.13) (Fig. 4.5, Table 4.5).

Table 4.5. Two-way ANOVA testing for effects of *Undaria* and mussel removal on the cover of total algal and canopy-forming algal cover. Degrees of freedom: *Undaria* = 1, mussels = 1, Undaria × Season = 1, residual = 16. Significant results are highlighted in bold

Response	**Test factor**	**SS**	**F**	**p**
Total algal cover 1/10/16	*Undaria*	3533.5	2.84	0.113
	Mussel	4819.6	3.87	0.068
	Undaria × Mussel	46.32	0.04	0.850
	Residual	18694		
Total algal cover 1/03/17	*Undaria*	50.88	0.04	0.852
	Mussel	5634.7	3.97	0.064
	Undaria × Mussel	0.22	<0.001	0.990
	Residual	22684		
Total algal cover 1/10/16	*Undaria*	181.8	0.23	0.638
	Mussel	189.1	0.24	0.631
	Undaria × Mussel	1061.4	1.34	0.264
	Residual	12647		
Canopy-forming algal cover 1/03/17	*Undaria*	840.7	1.94	0.184
	Mussel	2362.0	5.46	**0.034**
	Undaria × Mussel	168.7	0.39	0.542
	Residual	6488.6		
Canopy-forming algal cover 25/01/18	*Undaria*	2.38	0.01	0.912
	Mussel	491.0	2.60	0.126
	Undaria × Mussel	41.76	0.22	0.644
	Residual	3017.5		
Canopy-forming algal cover 25/01/18	*Undaria*	105.8	0.42	0.527
	Mussel	1248.2	4.93	**0.041**
	Undaria × Mussel	352.8	1.39	0.255
	Residual	4052.0		

Community analysis

A visual analysis of all samples (that were temporally non-independent) suggest that the community composition was very different at the final sampling date (which were entirely separated in PCO2 axis scores) (Fig. 4.6), whereas I found a large overlap between the first two sampling dates.

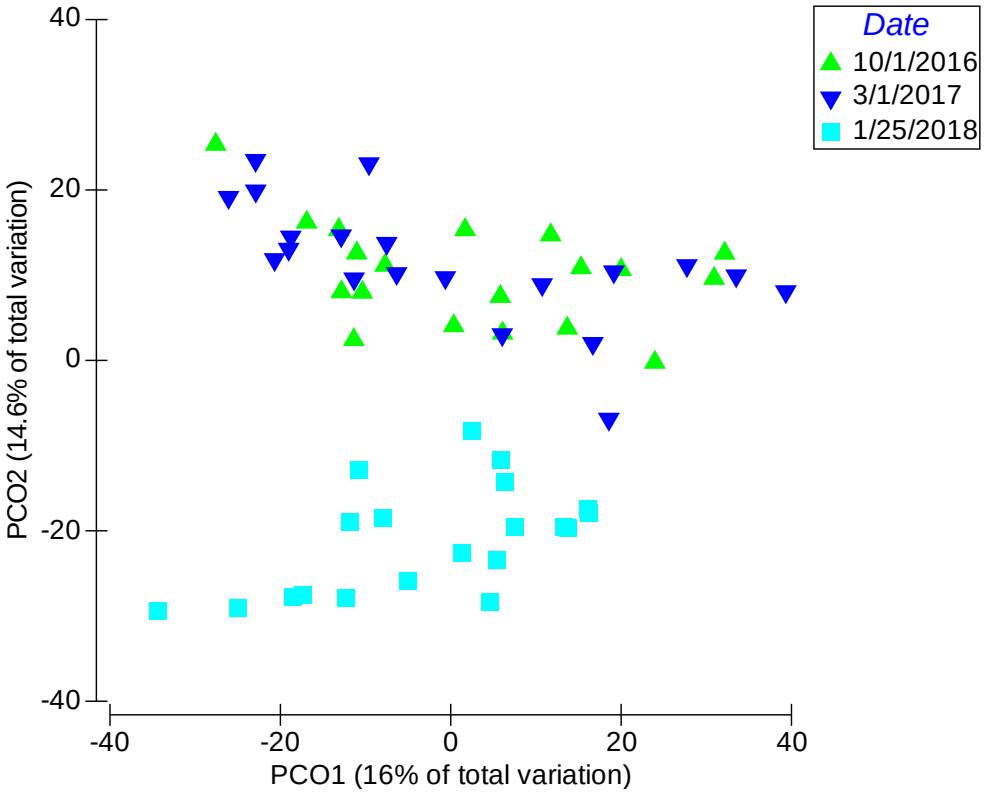

Figure 4.6. PCO plot of total community assemblages in experimental plots on different sample dates, including all experimental removal treatments. Data were square-root transformed and plotted using the Bray-Curtis similarity matrix.

There was no significant difference in the community composition of mobile invertebrates between *Undaria* or mussel removal treatments during any of the three surveys with the exception of mussel removal during the second survey (p=0.034) (Fig. 4.7, Table 4.6). Mussel removal had no significant effect on mobile invertebrate community in the first (p=0.096) and final (p=0.47) surveys (Fig. 4.7). *Undaria* removal treatment effects on the composition of the mobile invertebrates were not significant (p=0.24, 0.23, and 0.13 respectively) (Fig. 4.7, Table 4.6).

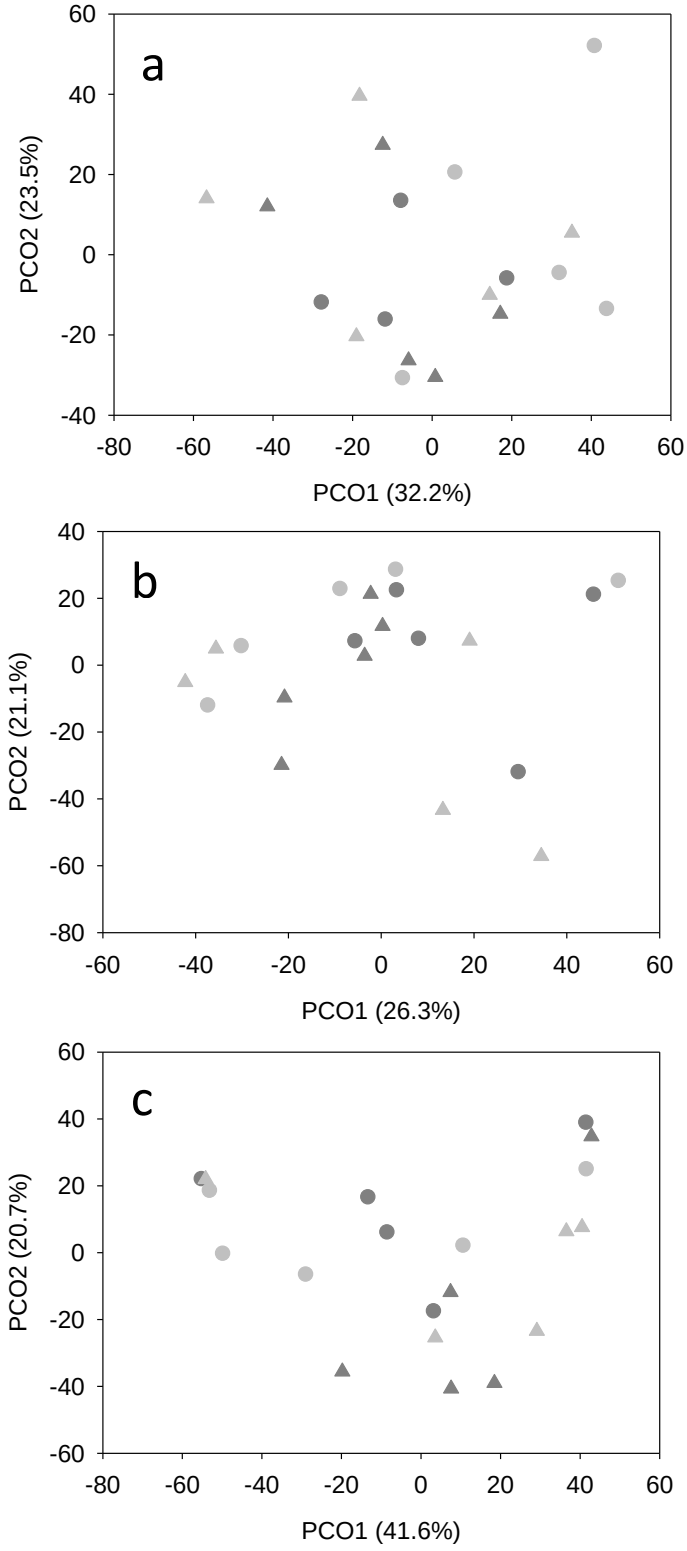

Figure 4.7. PCO plot of mobile invertebrate species on three sample dates; 1/10/16 (a), 1/3/17 (b), and 25/1/18 (c). Data were square-root transformed and plotted using the Bray-Curtis similarity matrix. Circle = *Undaria*, Triangle = *Undaria*-removal, Dark grey = Mussels, Light grey = mussel removal.

Table 4.6. Two-way PERMANOVA testing for effects of *Undaria* and mussel removal on multivariate community structure the cover of total algal and canopy-forming algal cover. Degrees of freedom: *Undaria* = 1, mussels = 1, *Undaria* × Season = 1, residual = 16. 4999 permutations. Significant results are highlighted in bold.

Response	**Test factor**	**SS**	**F**	**p**
Mobile community 1/10/2016	*Undaria*	3077.5	1.43	0.243
	Mussel	4169.1	1.94	0.096
	Undaria × Mussel	2394.3	1.11	0.351
	Residual	32317		
Mobile community 1/03/2017	*Undaria*	3446.5	1.40	0.23
	Mussel	5917.1	2.41	**0.034**
	Undaria × Mussel	3775	1.54	0.17
	Residual	39324		
Mobile community 25/01/2018	*Undaria*	5018.5	1.80	0.126
	Mussel	2672	0.96	0.469
	Undaria × Mussel	1747.7	0.63	0.681
	Residual	44582		
Sessile community 1/10/2016	*Undaria*	3299.2	2.50	**0.016**
	Mussel	3608.2	2.73	**0.006**
	Undaria × Mussel	838.7	0.64	0.774
	Residual	19803		
Sessile community 1/03/2017	*Undaria*	2935.8	1.93	0.069
	Mussel	2058.4	1.35	0.227
	Undaria × Mussel	1236.9	0.81	0.592
	Residual	24348		
Sessile community 25/01/2018	*Undaria*	646.0	0.50	0.892
	Mussel	2548	1.99	**0.042**
	Undaria × Mussel	975.0	0.76	0.653
	Residual	20527		

Sessile invertebrate and algal community composition varied more between removal treatments than for the mobile invertebrates. *Undaria* removal had a significant effect in the first community survey (p=0.016), but not in the second or third surveys (p=0.069, and 0.89) (Fig. 4.8). The sessile community was significantly different between mussel removal treatments in the first and third community surveys (p=0.006, and 0.042), but not on the second sampling date (p=0.28) (Fig. 4.8).

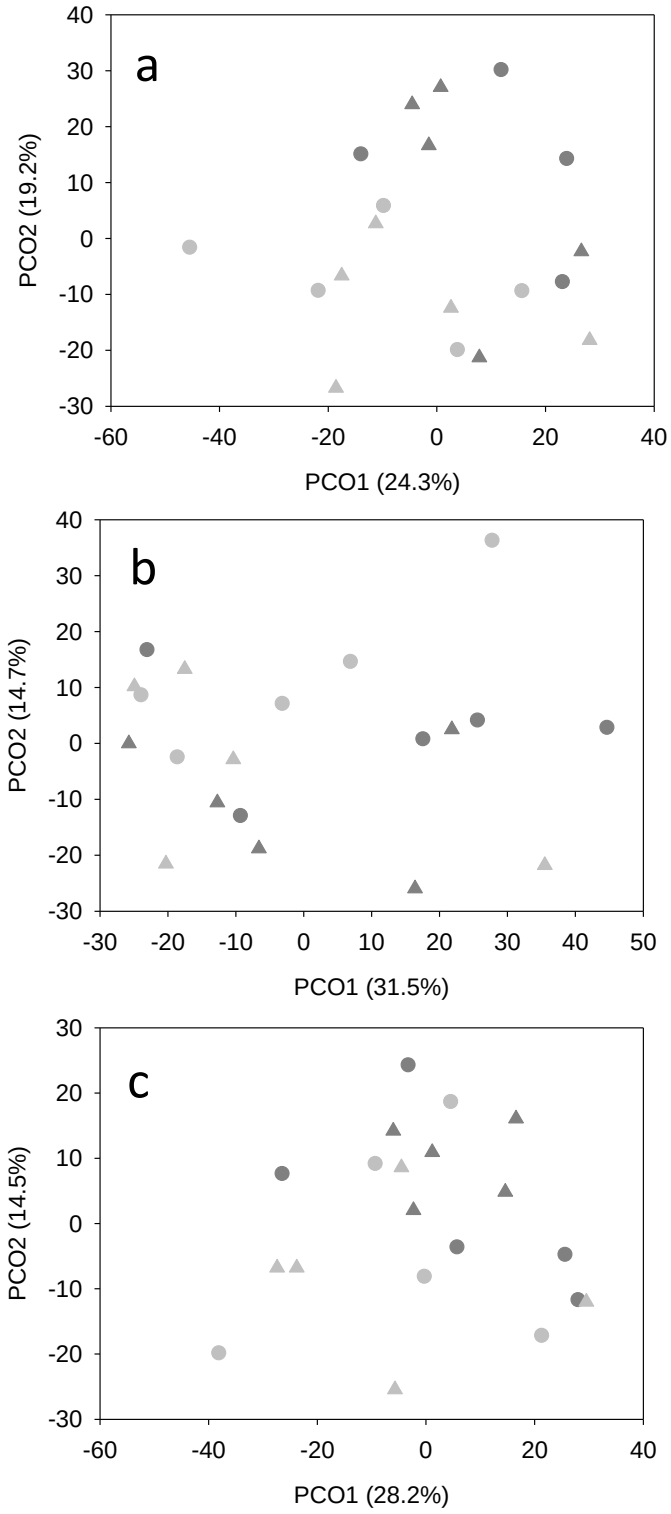

Figure 4.8. PCO plot of macroalgae and sessile invertebrate species on three sample dates; 1/10/16 (a), 1/3/17 (b), and 25/1/18 (c). Data were square-root transformed and plotted using the Bray-Curtis similarity matrix. Circle = *Undaria*, Triangle = *Undaria*-removal, Dark grey = Mussels, Light grey = mussel removal

The SIMPER (similarity percentage) analysis revealed that there was an average dissimilarity of 60% to 64% between sample dates (Table 4.7), 61% between *Undaria* removal treatments, and 62% between mussel removal treatments (Table 4.8). The taxa that contributed the most to the total dissimilarity varied between dates and removal treatments, but several taxa were frequently among those with the largest impacts. The brown algae *Carpophyllum maschalocarpum* and *Halopteris* spp. had dissimilarity of greater than 4% in all comparisons between groups (Table 4.7, Table 4.8). Both were more common where *Undaria* and mussels had been removed. Coralline algae were also frequently among the highest contributing taxa. *Corallina officinalis* and non-geniculate coralline algae contributed more than 4% of the total dissimilarity of all comparisons. *Corallina officinalis* was more common in plots where *Undaria* and mussels had not been removed. Non-geniculate coralline algae were more common in plots where *Undaria* had not been removed, and conversely where mussels had not been removed. The only invertebrate species that rated highly in dissimilarity was the barnacle *Chamaesipho columna*, which was in the top six contributing taxa in all comparisons (Table 4.7, Table 4.8).

Of the algal taxa identified in the community surveys, 22 of the 32 taxa (69%), and 17 of 50 (34%) of invertebrate taxa, had higher abundances in plots where *Undaria* had been removed. Of the algal taxa identified in the community surveys, 23 of the 32 taxa (72%), and 20 of 50 (40%) of invertebrate taxa, had higher abundances in plots where mussels had been removed. Overall algal taxa had higher abundances in disturbed plots and, conversely, invertebrate taxa had higher abundance in undisturbed plots.

Table 4.7. Results of SIMPER analysis on the percent cover of algal and sessile invertebrate species (square root transformed, Bray-Curtis similarity matrix), testing dissimilarity between sample dates, including all removal treatments. Only taxa that accounted for at least 4% of the dissimilarity were included. (n=20 plots per date)

Taxon	**Contribution (%)**	**Cumulative %**
Groups: 1/10/2016 & 1/3/2017	**Average dissimilarity = 60.31**	
Halopteris spp.	7.77	7.77
Carpophyllum maschalocarpum	6.31	14.08
Chamaesipho columna	6.18	20.26
Corallina officinalis	5.12	25.38
Non-geniculate coralline algae	5.03	30.41
Encrusting algae	4.90	35.31
Ralfsia verrucosa	4.71	40.02
Glossophora kuntii	4.54	44.56
Dictyota spp.	4.50	49.06
Groups: 1/10/2016 & 25/1/2018	**Average dissimilarity = 63.63**	
Non-geniculate coralline algae	7.97	7.97
Carpophyllum maschalocarpum	6.06	14.02
Paints	5.90	19.92
Chamaesipho columna	4.66	24.58
Halopteris spp.	4.36	28.94
Encrusting algae	4.23	33.17
Ralfsia verrucosa	4.06	37.23
Groups: 1/3/2017 & 25/1/2018	**Average dissimilarity = 63.92**	
Halopteris spp.	7.31	7.31
Non-geniculate coralline algae	6.29	13.59
Paints	6.02	19.61
Carpophyllum maschalocarpum	5.37	24.98
Corallina officinalis	4.93	29.91
Chamaesipho columna	4.71	34.62
Ralfsia verrucosa	4.58	39.20
Glossophora kuntii	4.51	43.71

Table 4.8. Results of SIMPER analysis on the percent cover of algal and sessile invertebrate species (square root transformed, Bray-Curtis similarity matrix), testing dissimilarity between *Undaria* and mussel presence, over all sample dates. The relative change in abundance when *Undaria* or mussels have been removed is listed as well. Only taxa that accounted for at least 4% of the dissimilarity were included. (n=30 plots per treatment)

Taxon	**Difference in abundance (%)**	**Contribution (%)**	**Cumulative %**
Groups: *Undaria*+ & *Undaria*-		**Average dissimilarity = 60.64**	
Halopteris spp.	+163	6.96	6.96
Carpophyllum maschalocarpum	+22	6.05	13.01
Non-geniculate coralline algae	-57	5.59	18.60
Chamaesipho columna	+67	5.20	23.79
Ralfsia verrucosa	+93	4.61	28.40
Corallina officinalis	-37	4.58	32.97
Encrusting algae	-43	4.40	37.37
Groups: Mussel+ & Mussel-		**Average dissimilarity = 61.72**	
Carpophyllum maschalocarpum	+128	6.32	6.32
Halopteris spp.	+26	6.19	12.51
Ralfsia verrucosa	-91	5.69	18.20
Non-geniculate coralline algae	+55	5.40	23.60
Chamaesipho columna	+123	5.12	28.72
Corallina officinalis	-46	4.66	33.38
Encrusting algae	+209	4.52	37.90

4.4 Discussion

Importantly, I found that mussels facilitated *Undaria* recruitment onto the reef. Furthermore, while no effects of *Undaria* or mussels were found on the richness or abundance of native algal species, the presence of mussels did have a negative impact on

the cover of canopy-forming algae. Neither *Undaria* or mussels affected the mobile invertebrate community, but the sessile community did differ during some of the sampling dates. However, the very hot summer of 2017-18 may have altered communities, as there were lower abundances of most species, and a different overall community structure in March 2018.

Undaria and mussel removal and recolonisation

Undaria's life history and biology mean that it is able to quickly colonise and establish in newly invaded areas, taking advantage of gaps that form in native algal cover. In this study, many *Undaria* individuals had settled on mussels, and the presence of mussels appeared to contribute to the colonisation of *Undaria*. In the monthly removals, more *Undaria* colonised plots where mussels were present than where no mussels occurred. *Undaria* has been shown previously to settle onto mussels (Thomsen unpublished, Chapter 2, 3), turf alga (Schiel and Thompson 2012, Thompson and Schiel 2012) and any hard substrate (Epstein and Smale 2017, South et al. 2017). These observations are consistent with the notion that mussels can facilitate the colonisation of algal species, act as ecosystem engineers, and as a substrate for algal attachment (Dittman and Robles 1991, Buschbaum et al. 2009).

Undaria's ability to remain dormant for extended periods of unfavourable conditions, and then, when more favourable conditions occur, its population can explode due to its fast growth, early maturation, and high reproductive output (Campbell et al. 1999, Schaffelke et al. 2005, Schiel and Thompson 2012, South et al. 2017). In fact, *Undaria* individuals are able to grow at a rate of 15 mm per day and reach lengths of one meter within 3 weeks (Thompson 2004). Under favourable conditions, dormant *Undaria* propagules can quickly become a large part of the macroalgal canopy-forming community, and due to its early maturation produce large amounts of further propagules. The combination of these factors means that, while *Undaria* may not appear to have any large impacts on existing healthy native macroalgal stands, any disruption of the existing canopy can be taken advantage of quickly, making it difficult for native algal species to recover (Epstein and Smale 2017, South et al. 2017).

Undaria and mussel removal treatments were successful at removing a large proportion of the abundance of both species within the plots where removals were applied. The first community survey was performed one month prior to the last removal treatment so can be used as a measure of how effective the treatments were. Mussels had effectively been eliminated from the quadrats where they were experimentally removed, dropping from 70% cover in un-manipulated plots to an average cover of less than 5%, an effective reduction of 90%. *Undaria* was more difficult to control as it can recover quickly, especially during the winter months when it grows the fastest. In addition to this, if a wide enough margin around the *Undaria* removal plots is not maintained, large *Undaria* individuals from outside the plot may be placed inside it by wave action, so even if there are no *Undaria* holdfasts within a plot, there may still be some canopy effects from very large adjacent individuals. As a result of this *Undaria* removal may not have been as effective in reducing *Undaria* cover to the same degree that mussels were controlled, only reducing it from 80% to 40%, an overall reduction of 50%. This may have contributed to the lack of significant differences between *Undaria* removal treatments.

Percent cover and richness of algal and invertebrate species occurring in plots

The third survey in January 2018 showed significant drops in the abundance and cover of almost all algal and invertebrate taxa. It is not clear what caused this decline but it possible that it is the result of abnormally high sea water temperature that occurred over the summer 2017/18, i.e. in-between sampling date 2 and 3. During that time, New Zealand's coastal waters experienced very high sea surface temperature anomalies of up to 6 degrees C above the historical monthly average and about +2 degrees C in coastal Canterbury (NIWA 2018). However, it is also possible that this drop was caused by other factors, like a large storm or unusual high turbidity levels.

As discussed above, *Undaria* has an immense ability to recover after the habitat has been disturbed and exploits gaps in the canopy have formed (South et al. 2017). *Undaria* itself was much less abundant in March 2018, with cover dropping from 80% in plots where *Undaria* was not removed one year before hot summer to 10% in plots where *Undaria* had not been removed the following year. Regardless of this dramatic drop in cover, subsequent visits to

Pile Bay 2-3 months after the unusually warm summer revealed that *Undaria* had recovered and was then present in areas on the reef where it had historically not been found. Pile Bay previously had a few dense stands of southern bull kelp, *Durvillaea poha*, which had almost vanished (Thomsen et al. 2018). *Undaria* has since populated these areas in addition to the rest of the reef where it had been present earlier (Thomsen, unpublished data).

A number of factors likely to affect algal communities, including water temperature, wave exposure, risk of desiccation, grazing, and in some cases allelopathy by other algal species (Underwood 1980, Jernakoff 1983). My results in general agree with other studies that have examined the impact of *Undaria* on existing algal communities. As with this study, other studies reported no significant effect of the introduction or removal of *Undaria* on the diversity or abundance of native algal species (Valentine and Johnson 2003, Schiel and Thompson 2012, South et al. 2016). As with the total algal cover, *Undaria* removal had no significant effect on the cover of canopy-forming macroalgal species, even though these species would be expected to occupy a similar niche.

While *Undaria* and mussel removal treatments generally had no effect on the richness or abundance of algal species, there was a significant difference in the cover of canopy-forming macroalgal species between plots where mussels were present and where mussels had been removed, during the initial and final community surveys. Excluding *Undaria*, the cover of canopy-forming species was lower in plots where mussels were present. This may be because *Undaria* is better able to settle into established mussel beds than the other macroalgal species. Alternatively, *Undaria* may be more suited to the areas with higher wave exposure, where mussels are already in higher abundance, than the native macroalgal species.

In the presence of mussels, average invertebrate richness was found to be higher. Mussels have been shown to provide secondary substrate for other species to attach to, and reduce the effects of wave exposure and desiccation (Borthagaray and Carranza 2007). Similar findings have been reported in other studies (Valdivia and Thiel 2006, Borthagaray and Carranza 2007, Silliman et al. 2011), and because of their facilitative role, mussels are often considered ecosystem engineers (Buschbaum et al. 2009, Bateman and Bishop 2017). In my study the difference in invertebrate richness was largely due to a number of colonial bryozoan and hydrozoan species which were much more commonly found in association

with mussels. Several gastropod species were also more abundant in plots where mussels were present; specifically, *Haustrum haustorium*, *Buccinulum* spp., *Notoacmea parviconoidea*, *Cellana radians*, and *Siphonaria* spp. Whelks are known to feed on mussels and many of the other snails found between them (Luckens 1975), so it is not surprising that whelks were more commonly found in association with mussels.

The only commonly found invertebrate that had higher average abundance in plots where mussels had been removed was the barnacle *Chamaesipho columna*. While barnacles are capable of settling onto mussels (see chapter 3), they are more frequently found settling directly onto bare rock, such as in the areas where mussels had been removed. *Chamaesipho columna* was also more abundant in plots where *Undaria* had been removed, further lending evidence to the idea that it does better without the company of larger sessile biota.

Invasive species can increase the abundance and richness of epifaunal communities where they create a more physically complex habitat (Sellheim et al. 2010). I have found an increase in the number of smaller invertebrates (e.g. isopods) associated with mussels in the presence of *Undaria* (see chapter 3), where *Undaria* greatly increased the available attachment and shelter area relative to the mussels it is attached to. But when the larger ecosystem scale is considered, then this apparent increase in invertebrates was not significant.

The lack of a difference in the number of invertebrate species between *Undaria* removal treatments reflects the findings of another study. Migné et al. (2015) found that the removal of a different canopy-forming species (*Fucus serratus*) did not affect invertebrate richness, although it had negative impacts on several ecosystem characteristics such as primary productivity and respiration, as well as invertebrate abundance. Overall community, algal abundance and community structure, and invertebrate richness did not differ. Invertebrate abundance was greatly decreased by canopy removal (Migné et al. 2015). Other studies found *Undaria* to have numbers of associated invertebrates that were similar to native macroalgal species with comparable seasonality and physical complexity (Suárez Jiménez 2015, Arnold et al. 2016). Several of these and other *Undaria* associates were shown to graze on *Undaria*, both in New Zealand and overseas (Sinner et al. 2000, Thornber et al. 2004, Teso et al. 2009, Suárez Jiménez et al. 2015).

Community analysis

Almost all algal and invertebrate species were greatly reduced in abundance in the last survey in January 2018. This may be related to increased sea temperatures in the summer 2017-18 but could also be caused by other factors such as significant storms and wave action or high turbidity. Although it is not possible to refer to any corresponding control (non-heatwave) data for comparison, the unusual temperatures that occurred between the second and third survey could be a plausible factor in the substantial changes that were observed over this period. Heatwaves have been recorded to drive significant changes in community structure overseas as well (Garrabou et al. 2009, Wernberg et al. 2016, Oliver et al. 2017). Increasing sea surface temperature is already shifting environmental conditions to the margins or outside the tolerance of native species, especially when these conditions persist for an extended period.

In the present study, the changes in the community between the second and third survey, whatever caused this, masked some of the effects of the removal treatments on the algal and invertebrate communities by reducing the difference in *Undaria* and mussel cover between the non-removal and removal treatments, and by reducing the overall cover of the measured species. However, as with other studies (Migné et al. 2015, South et al. 2016), removal treatments did not lead to significant effects of community composition in most cases.

Mobile invertebrates, especially highly mobile groups such as crabs, can be difficult to accurately measure in variable environments like the intertidal zone. While sessile organisms remain in experimental plots regardless of tidal state, mobile organisms can simply follow the ideal environmental conditions, often emerging from cover during high tide to feed, before returning to whatever cover, mussel or otherwise, they find themselves closest to. This means that the surveys performed during low tide may not be entirely representative of the actual community.

In theory, grazers are likely to be one of the groups most affected by *Undaria* presence. In New Zealand they have been shown to feed on *Undaria* just as often as on native species (Sinner et al. 2000, Suárez Jiménez et al. 2015). However, I found that there was little difference in their abundance between *Undaria* treatments. The most abundant grazers,

Lunella smaragdus, *Notoacmea parviconoidea*, and *Margarella* spp., were all found more or less equally often in plots where *Undaria* had or had not been removed. This may be due to grazers not showing any preference toward *Undaria* or native algal species, or alternatively, that *Undaria* removal did not reduce its cover to a sufficient degree to produce changes in associated grazers.

Unlike the mobile invertebrates, there was a change in the sessile invertebrate and algae community between *Undaria* and mussel removal plots. *Undaria* removal was associated with a significant change in community composition in one of the community surveys, and mussel removal was in two community surveys. This is due to a number of algal species that were very rare in plots where *Undaria* and mussels had not been removed, such as *Carpophyllum maschalocarpum*, and *Cystophora scalaris*. Additionally, as discussed earlier, barnacles were also more abundant in plots where *Undaria* and mussels had been removed.

Many of the algal species could be classified as habitat-forming or at least not as dependent on the presence of other taxa for their survival. This was different for invertebrate species which are more vulnerable to predation or desiccation without the presence of existing habitat-forming species including mussels and canopy-forming macroalgae.

Overall, this study shows that, similar to what other studies have found, *Undaria* has a limited impact on the algal communities it invades. Although native grazers have been found to feed on *Undaria*, the presence of *Undaria* had no noticeable effect on the invertebrate community. This suggests that other habitat-forming species and environmental conditions have a more important role in determining community composition than *Undaria*. I found that an existing habitat-former, the dense mussel beds found on many reefs and artificial structures in New Zealand, may facilitate the invasion of non-native species such as *Undaria*.

5 General discussion

The Asian kelp *Undaria pinnatifida* is one of the most successful marine invasive species. It has been extensively studied and many scientific papers have been published on *Undaria*'s distribution, phenology, physiological characteristics, population demography, and its behaviour and effects as an invasive species (Epstein and Smale 2017, South et al. 2017). However, even with this existing research, I am not aware of any specific studies that examined *Undaria*'s interactions with mussels and mussel reefs, with which *Undaria* is commonly associated in New Zealand, and despite the considerable ecological and economic importance of mussels. Therefore, I tested hypotheses about the nature of *Undaria*'s apparent association with mussels and their possible environmental preferences and potential facilitation mechanisms, *Undaria*'s impacts on recruitment and health (condition index) of mussels and *Undaria*'s effects on mussel-associated invertebrates and seaweed. In this final chapter I will discuss and highlight the major findings of my research, whether they support my hypotheses, and what their theoretical and practical implications are.

Undaria distribution, abundance, and habitat use in Lyttelton Harbour, and its apparent association with mussels

The results of my studies on the distribution and abundance of *Undaria* in Lyttelton Harbour (Chapter 2) confirm that it has great invasion potential and is able to succeed and become highly abundant in a range of environmental conditions. Established populations on almost all continents reflects its success as a prolific marine invader (Curiel et al. 2002, Silva et al. 2002, Casas et al. 2004, South et al. 2017). Given the length of time *Undaria* has been present in Lyttelton Harbour (ca. 30 years since it was first reported in 1988), it is not surprising that populations were found at every reef sampled. *Undaria* was especially common in the eastern half of Lyttelton Harbour, towards the Harbour entrance, which is dominated by semi-exposed rocky reefs.

Undaria has several characteristics that contribute to its success as a non-native species that is now widespread in invaded areas. These include a high settlement rate on ships' hulls by

which it can be transported between continents, its ability to remain dormant for extended periods of unfavourable conditions, and its fast growth, early maturation, and high reproductive output when conditions are more favourable (Campbell et al. 1999, Schaffelke et al. 2005, Schiel and Thompson 2012, South et al. 2017). Undaria is the only kelp in New Zealand that creeps up into the lower mid-tide zone whereas all native kelps are permanently subtidal and have little or no desiccation resistance. *Undaria* is well-acclimatised to the conditions of the low intertidal and lower mid-tide zones and this makes it a potential competitor with native species occurring in these intertidal zones.

My survey results (Chapters 2) showed that *Undaria* was found extensively in the low intertidal zone (note, however, that I did not sample the subtidal zone where its largest populations usually are (Suárez Jiménez 2015)), and its highest densities were in the same tidal zone where mussels were most common. Both *Undaria* and mussels are vertically restricted in the intertidal zone by their vulnerability to desiccation and their requirement for access to nutrients when submerged (Kennedy 1976, Bollen et al. 2017). The survey data showed that in the low intertidal zone *Undaria* and mussels were found co-occurring more frequently than either was found by themselves. This suggests that the two species either share preferences for similar habitats, or that one species may be facilitating the other. There was also a positive relationship between the cover of mussels and *Undaria*, with a relatively weak relationship on the scale of small quadrats but a stronger relationship at the scale of whole reefs. In a removal experiment (Chapter 4) I did not find any difference in *Undaria* cover between mussel removal treatments and controls, but this was during the peak *Undaria* season where cover was high across the reef (Chapter 2). Therefore, these findings do not disagree with my other survey data. Overall, there is indeed an apparent spatial association between *Undaria* and mussels in the low intertidal zone. Furthermore, at the smallest scale of individual *Undaria* plants I found that *Undaria* are often growing directly on mussels (there was a significant positive relationship between mussel and *Undaria* cover (Chapter 2)), which is further contributing to their co-occurrence patterns. *Undaria* has been shown to be able to settle on almost any hard substrate, mussels included (Hay 1990, Forrest and Blakemore 2006, Sliwa et al. 2006). Other mytilid mussels have been shown to provide secondary substrate for other species that are attached to them (Dittman and Robles 1991, Buschbaum et al. 2009), which leads to increased species richness of

communities in the intertidal zone (Borthagaray and Carranza 2007). This effect of mussels is probably due to a reduction in detrimental wave exposure and desiccation, compared with patches where mussels were absent. My removal experiment (Chapter 4) showed that while there was no difference in *Undaria* cover between mussel removal treatments and controls, there was an increased rate of *Undaria* recruitment in plots where mussels were present. I was unable to determine the exact mechanisms through which mussels were able to increase *Undaria* recruitment, but these observations are consistent with previous studies.

Mussel and wave exposure effects on *Undaria's* seasonality

Undaria's typical seasonality, with peak cover and large sporophyte size in winter followed by senescence during summer (Hay and Villouta 1993, Morita et al. 2003, James and Shears 2012), has previously been observed in Lyttelton Harbour (Schiel and Thompson 2012, Thompson and Schiel 2012, South et al. 2016) and was further confirmed in my study (Chapter 2). However, my data also indicated that the decrease in *Undaria*'s abundance outside of the peak winter season occurred to a lesser degree when it was associated with mussels. This suggests that in situations when *Undaria* is associated with mussels, it may be able to remain at relatively high abundance even when cover in nearby areas without mussels has decreased and the large sporophytes are largely absent due to senescence. This could in part be due to the nature of the more wave-exposed areas where *Undaria* and mussels co-occur. *Undaria* has previously been shown to succeed in areas with high wave exposure (Castric-Fey et al. 1993, Nanba et al. 2011, Peteiro and Freire 2011, James and Shears 2016b). Increased wave action may lead to greater propagule arrival, increased nutrient supply, reduced risk of desiccation during low tide, less consumer pressure, reduced temperature fluctuations and sediment accumulation, all of which would benefit increased settlement, growth and survival (Hurd 2000). Conversely, areas with high wave exposure are likely to cause an increased rate of dislodgement of mature sporophytes. However, because *Undaria* can have multiple cohorts of recruits (Thornber et al. 2004, Thompson and Schiel 2012), and removal of the adult *Undaria* canopy has been shown to trigger the growth of dormant propagules (Thompson and Schiel 2012), potentially by reducing competition for light, the removal of *Undaria* individuals by waves could facilitate further recruitment. This would especially be the case in areas with dense mussel beds if mussels are able to facilitate

Undaria recruitment as suggested above. Increased opportunities for settlement throughout the year, for example, might increase the number of *Undaria* cohorts, and thereby prolong the cover of mature *Undaria*.

Undaria effects on mussel condition

Mussel condition is typically assessed using the condition index (CI). However, when considering the effects of *Undaria* on the CI of green-lipped mussel (*Perna canaliculus*) it is important to keep in mind that *Perna*'s CI changes across the seasons. The lowest CI values typically occur in spring (Hickman and Illingworth 1980, Fox 2003, Lachowicz 2005), a pattern I also found for *Perna* in Lyttelton Harbour (Chapter 3). Importantly, the presence of *Undaria* led to a consistent and significant reduction of *Perna*'s CI (by ca. 20% across seasons). This reduction could have been caused by several factors. *Undaria* presence on mussels could lead to reduced mussel growth either through obstruction of temperature regulation or reduced ability of filter-feeding, as suggested by Dittman and Robles (1991) for other mussels. The effect on *Perna's* CI that I observed is new because, although there are several studies testing for effects of environmental factors on both growth and CI of mussels (e.g. Hickman and Illingworth 1980, Marsden and Weatherhead 1999, Orban et al. 2002, Lander et al. 2012, Chandurvelan et al. 2016), studies examining the effect of biological factors, such as epiphytes, have only assessed impacts on mussel growth, not CI (Dittman and Robles 1991, de Sá et al. 2007). These studies have, for example, shown that the California mussel *Mytilus californianus* had lower growth rates when it was covered with red algal epiphytes (Dittman and Robles 1991). Likewise, the brown mussel *Perna perna* was significantly smaller in aquaculture when epiphytes and other fouling organisms were allowed to grow than when they were removed every month (de Sá et al. 2007). Reduced growth of other bivalves caused by epiphytic algae was also reported by Enright et al. (1983). Conversely, studies in Ireland found that epiphytic algal mats (of *Fucus* and other epiphytic algae) had no effect on mussel growth (O'Connor et al. 2006, O'Connor 2010).

Reduced growth and CI of overgrown mussels could also be explained by increased energetic investment in byssal threads. For example, blue mussels (*Mytilus edulis*) have been shown to increase byssal thread production in response to fouling by limpets (Thieltges and

Buschbaum 2007) and artificial epibionts (Garner and Litvaitis 2017). Such increased energetic costs could therefore potentially contribute to a reduction in mussel CI. Furthermore, epibionts were shown to greatly reduce the rate at which juvenile mussels could move and relocate themselves within a reef, which may be important to locate the best feeding microsites (Garner and Litvaitis 2017).

Which of these outlined mechanisms ultimately affected *Perna's* CI cannot be determined from my study, and more controlled experiments at mussel reefs or in the laboratory would be required to identify them. Further studies focusing on specific physiological mussel traits, such as reproductive tissue weight, filtration rates, absorption rates, stress-proteins and respiration rates, might also help to identify the mechanisms through which *Undaria* affect mussels. Nevertheless, my results clearly show that *Undaria* growing on mussels causes a moderate reduction in *Perna* condition index.

Effects of *Undaria* and mussels on algae, sessile invertebrate species and the community of sessile organisms

Surprisingly, there were no noticeable effects of *Undaria* presence on sessile epibiota (Chapters 3 and 4). This may be because many of the other algal species and sessile invertebrates commonly found on mussels and on mussel reefs are slower growing than *Undaria*. Consequently, native sessile species were likely to be present before *Undaria* settled and would probably survive for 5-8 month corresponding to the typical life span of an *Undaria* holdfast (Schiel and Thompson 2012). The only species that appeared to be affected by *Undaria* was *Corallina officinalis* which was more abundant in the presence of *Undaria*. This may be because *Undaria* has high settlement rates on coralline turf substrates (Schiel and Thompson 2012, South et al. 2016, South and Thomsen 2016). Therefore, the positive association between *C. officinalis* and *Undaria* is probably caused by *Undaria* responding to *C. officinalis*, rather than the opposite.

My results are consistent with other studies that also have reported no, or few, significant effects of *Undaria* on the diversity and abundance of native algal species (Valentine and Johnson 2003, Schiel and Thompson 2012, South et al. 2016). In other words, I found no effects of *Undaria* removal on the cover of canopy-forming macroalgal species, even though

these species would be expected to occupy a similar niche. However, while *Undaria* may appear not to have any large impacts on existing healthy native macroalgal stands, *Undaria* may be able to benefit from disturbances to the existing canopy as it can quickly occupy vacant habitat (Epstein and Smale 2017, South et al. 2017, Schiel et al. 2018). For example, this appeared to be the case in parts of Pile Bay where *Undaria* invaded areas were southern bull kelp *Durvillaea poha* disappeared over the summer of 2017-18 (Thomsen et al. 2018), as well as in Moeraki where a clear tipping point was identified after which the community quickly became dominated by *Undaria* (Schiel et al. 2018).

While *Undaria* and mussel removal treatments generally had no effect on the richness or abundance of algal species, there was significantly greater cover of canopy-forming macroalgal species in plots where mussels were present than where mussels had been removed (Chapter 4). This may be because *Undaria* is better able to settle into established mussel beds than the other macroalgal species. Alternatively, *Undaria* may be more suited to the areas with higher wave exposure, where mussels are already in higher abundance, than the native macroalgal species.

In some cases there was an effect of *Undaria* and mussel removal treatments on the overall multivariate community structure of sessile invertebrate and algae (Chapter 4). These community-wide effects were due to a number of algal species that were rare in the plots where *Undaria* and mussels had not been removed, (e.g., *Carpophyllum maschalocarpum* and *Cystophora scalaris*). In addition, barnacles were also more abundant in plots where *Undaria* and mussels had been removed.

Effects of *Undaria* and mussel presence on mobile invertebrates

Undaria had the greatest effects on communities of mobile invertebrates. For example, I found that the presence of *Undaria* increased species richness and abundances of mobile invertebrates associated with individual mussels (Chapter 3). This increase was associated with particularly high abundances of small amphipods and isopods inhabiting the complex biogenic holdfast structure, while larger snails, limpets, and the porcelain crab *Petrolisthes elongatus* increased in abundance but to a smaller degree. This may be evidence of mussels and *Undaria* driving a 'habitat cascade' (Thomsen et al. 2010), where mussel reefs facilitate

Undaria, which in turn facilitates the diversity and abundance of the invertebrate community associated with *Undaria*. My result is supported by previous studies which also have found relatively high abundance and richness of invertebrates associated with invasive *Undaria* (and other invasive seaweeds) (Schmidt and Scheibling 2006, Suárez Jiménez 2015, Arnold et al. 2016). The physically complex structure of the *Undaria* holdfast and sporophyll (compared with mussel patches without *Undaria*) may play a large role in the increased abundance of invertebrates as these biogenic structures can provide shelter for smaller invertebrates such as isopods (Anderson et al. 1997, Thiel and Vásquez 2000, Sellheim et al. 2010, Tuya et al. 2011). It is also possible that *Undaria* is an important food source, as I found high abundances of grazing snails and limpets. I did not examine whether these groups were grazing on the *Undaria* itself or on the biofilm that forms on its surface, but native grazers have previously been shown to feed on *Undaria* in New Zealand (Sinner et al. 2000, Suárez Jiménez et al. 2015).

Contrary to my study on individual mussels (Chapter 2), I did not find any substantial effect of *Undaria* on either the richness of mobile invertebrate species, or the overall mobile invertebrate community structure. This differed from the results of my smaller scale experiments because the small-scale study (Chapter 3) explicitly sampled cryptic organisms hiding within the holdfasts (destructive sampling) whereas the community analysis (Chapter 4) only focused on the organisms that are visible in field surveys (non-destructive sampling). The changes in cryptic organisms would not be observed due to the difficulty of finding them in the field, and the limited amount of time available for surveys in the low intertidal zone. Migné et al. (2015) also found that the removal of a different canopy-forming species (*Fucus serratus*) had no effect on invertebrate richness. This suggests that the most important driver is not so much the type of canopy-forming algae but rather the amount of total canopy cover. Invasive species have been shown to increase the abundance and richness of epifaunal communities where they create a more physically complex habitat (Sellheim et al. 2010); this is also the case when mussels and *Undaria* grow together. The lack of community-wide effects may also be due to reef-wide decreases in community abundance towards the end of my study, which may have obscured or masked any real effects of *Undaria* on the mobile community.

While *Undaria* was found to have some effects on the invertebrate community, the presence of mussels had a stronger effect on the overall invertebrate community than did *Undaria*. Higher invertebrate richness and abundances in the presence of mussels have been reported in several other studies (Valdivia and Thiel 2006, Borthagaray and Carranza 2007, Silliman et al. 2011). Mussels are often considered important habitat-forming species because of their ability to ameliorate adverse environmental conditions and protect invertebrates from predation (Buschbaum et al. 2009, Bateman and Bishop 2017). Dense mussel canopies may provide more consistent shelter than macroalgal species which move with tidal changes, often only have small simple holdfasts and/or shorter lifespans. While the biogenic habitat provided by *Undaria* may be comparable to the other macroalgal species in Lyttelton Harbour, it is likely that mussels provide a more complex and more stable habitat that is conducive to a richer invertebrate community.

One of the caveats of my study is that sampling was performed only in the intertidal zone at low tide. It was therefore not possible to determine whether collected invertebrates are also associated with *Undaria* and mussels when they were submerged during high tide (or simply are using these habitats for shelter at low tide). Importantly, in this study, the distribution and effects of *Undaria* have not been investigated for subtidal populations. Furthermore, I only investigated relationships between *Undaria* and mussels on reefs within Lyttelton Harbour. Future studies should search for similar patterns in other locations to increase the generality of my findings.

Comparison of my hypotheses and the overall findings

To sum up my results; I initially outlined five specific hypotheses

First, I hypothesized that *Undaria* will be more abundant in association with mussels than in areas where mussels are absent because they prefer similar environmental conditions (tidal level and wave exposure among others) (Chapter 2, Chapter 4);

Collectively my findings confirm my hypothesis that *Undaria* and mussels are often found together in the low intertidal zone of Lyttelton Harbour. I have been able to demonstrate that *Undaria* is not only frequently attached directly to mussels or in close association with mussel beds on reefs, but *Undaria* was also found more frequently with mussels than any of

the native canopy-forming algal species. This means that *Undaria*‘s impact on native mussel reefs is common and widespread, and that its impacts on mussels are likely to be different from those of native seaweeds.

Second, I hypothesized that *Undaria* exhibited reduced seasonal variation when associated with mussel reefs, as this microhabitat may facilitate more persistent populations of mature *Undaria* (Chapter 2);

I found that *Undaria* was able to remain at relatively high abundances outside of its normal growth period when in association with mussels. This may be due to facilitative effects of mussels on *Undaria*, whereby they reduce the effect of adverse conditions during the senescence season. Alternatively, this change in *Undaria*’s phenology may be due to a more suitable environmental conditions that occur in the microhabitat where mussels and *Undaria* overlap.

Third, I hypothesized that *Undaria* has a negative impact on mussels, mussel condition index and on sessile epibiota (through competition for space) but positive effects on mobile invertebrates (through habitat-provisioning) (Chapter 3);

I was able to demonstrate a negative impact of *Undaria* on the condition of mussels, which are important habitat-formers on the reef. *Undaria* individuals affected the condition of mussels to which they are attached, which may reduce the mussels’ ability to withstand adverse environmental conditions, and potentially decrease their reproductive output. This could have negative long-term effects on the overall health of the mussel reef. However, there was no indication that *Undaria* presence had a negative impact on mussel recruitment, based on the results of removal experiments.

I found mixed effects of *Undaria* on the associated algal and invertebrate communities. *Undaria* did not have any detectable effects on sessile organisms attached to mussels, although it is possible that *Undaria* could be shading other seaweeds. However, the short life-span of individual *Undaria* plants may limit their effects on the abundance of other sessile species.

As hypothesized, *Undaria* had a significant positive effect on the abundance of mobile invertebrates, especially smaller species that are able to shelter within the *Undaria* holdfast. These invertebrates were much more species-rich and abundant where *Undaria* was present, and this could have trophic effects on predators of these invertebrates. Overall, in the short term, *Undaria* may have significant positive effects for the reef community because it is highly abundant, has high net primary production, and may facilitate flow-on effects.

Fourth, I hypothesized that mussels increase *Undaria* recruitment (through stress-reduction), and, conversely, *Undaria* limits mussel recruitment (through space occupation) (Chapter 4);

My data suggest that the rate of *Undaria* recruitment was indeed greater in the presence of mussels, based on the comparison of mussel plots and mussel removal plots. I did not investigate the exact mechanisms through which this occurred, but it is likely that this is driven in part by the mussels themselves rather than differences in environmental conditions, as the experimental design with adjacent mussel treatment plots minimised environmental effects on recruitment. Mussels may be able to increase the rate at which *Undaria* recruits by protecting juveniles from desiccation, excessive wave-action, and grazing.

Finally, I hypothesised that the algal and invertebrate communities differ between plots where *Undaria* and *Perna* have been removed, compared to un-manipulated control plots (Chapter 4).

At the community scale, my results indicate that *Undaria* had only minor effects on the reef community. The presence of *Undaria* did not have any noticeable effect on the abundance of other algal species or invertebrates, and only rarely did it have an impact on the overall reef community composition. However, it must be noted that in the longer term, *Undaria* could potentially cause a shift in community structure by preventing the recovery of native algal communities if they become disturbed, as *Undaria* can fill any gaps in the algal canopy.

Applied implications of my findings

This study may have implications for the control and management of invasive species partly because my results suggest that it is important to prevent arrivals of new invaders (because when arrived *Undaria* was an extremely efficient recruiter and space occupier), but also because it highlights that invasive species may have better than expected performance outside of their native range. For example, for *Undaria*, it would not be sufficient to study its ecology in its native range to understand its success in a newly introduced region (e.g. I am not aware of any studies on *Undaria*-mussel interactions from its native region). Rather, it would be very interesting to compare its ecology in both its native and invaded ranges. While not investigated in this study, it is possible that *Undaria* has other effects, for example through indirect competition; many native grazers feed on *Undaria* (Sinner et al. 2000, Suárez Jiménez et al. 2015) and *Undaria* could therefore indirectly affect other native seaweed species by supporting large populations of herbivores. Thus, *Undaria* can both have negative community impacts when it first becomes established but can also have positive effects through increasing primary productivity and habitat provision for native invertebrates.

Effects of *Undaria* directly on *Perna* have not been studied even though *Undaria* is a common fouling species on artificial structures including mussel aquaculture lines. I was able to show that *Undaria* can have a negative impact on the condition of mussels. Mussels are cleaned of epibionts before they are sold, but the mussel lines themselves may not be frequently cleaned of epibiont fouling, and could therefore have attached *Undaria* for an extended part of their growth cycle (Woods et al. 2012). Economically, this could mean that mussels would not reach the same size after the same length of culturing time, may taste differently, or could look less appealing. All of these changes could decrease the sale value of the mussels, which potentially wider financial ramifications across the large existing aquaculture industry in New Zealand (Woods et al. 2012, Fletcher 2013).

Conclusions

In conclusion, this study documents that the invasive kelp *Undaria* was more frequently found in the presence of native mussels than not, at a large Harbour scale, medium reef scale, and small individual plant scale. My experimental data suggested that mussels may facilitate *Undaria* as mussels increased recruitment and reduced seasonal variation of *Undaria*. This was followed by an apparent 'habitat cascade', where *Undaria* (in particular its holdfasts) facilitated mobile invertebrates. Furthermore, while previous studies have not found many negative impacts of *Undaria* on the native reef communities, I identified a negative effect on the native mussel *Perna* to which it frequently attaches. Finally, my results suggest that previously undocumented *Undaria*-mussel interactions, may have implications for the management of invasive marine species and established aquaculture processes.

6 Literature cited

Albrecht, A., and K. Reise. 1994. Effects of *Fucus vesiculosus* covering intertidal mussel beds in the Wadden Sea. Helgoländer Meeresuntersuchungen **48**:243-256.

Albrecht, A. S. 1998. Soft bottom versus hard rock: Community ecology of macroalgae on intertidal mussel beds in the Wadden Sea. Journal of Experimental Marine Biology and Ecology **229**:85-109.

Anderson, M., R. N. Gorley, and K. Clarke. 2008. PERMANOVA+ for primer: Guide to software and statistical methods. PRIMER-E, Plymouth.

Anderson, R., P. Carrick, G. Levitt, and A. Share. 1997. Holdfasts of adult kelp *Ecklonia maxima* provide refuges from grazing for recruitment of juvenile kelps. Marine Ecology Progress Series **159**:265-273.

Arnold, M., H. Teagle, M. P. Brown, and D. A. Smale. 2016. The structure of biogenic habitat and epibiotic assemblages associated with the global invasive kelp *Undaria pinnatifida* in comparison to native macroalgae. Biological Invasions **18**:661-676.

Baird, R. 1958. Measurement of condition in mussels and oysters. ICES Journal of Marine Science **23**:249-257.

Baird, R. H. 1966. Factors affecting growth and condition of mussels (*Mytilus edulis* L.). Fishery Investigations. Series 2 **25**:1-33.

Bateman, D. C., and M. J. Bishop. 2017. The environmental context and traits of habitat‐forming bivalves influence the magnitude of their ecosystem engineering. Marine Ecology Progress Series **563**:95-110.

Battershill, C., K. Miller, and R. Cole. 1998. The understory of marine invasions. Seafood New Zealand **6**:31-33.

Bax, N., A. Williamson, M. Aguero, E. Gonzalez, and W. Geeves. 2003. Marine invasive alien species: a threat to global biodiversity. Marine Policy **27**:313-323.

Bertness, M. D., G. C. Trussell, P. J. Ewanchuk, B. R. Silliman, and C. Mullan Crain. 2004. Consumer-controlled community states on Gulf of Maine rocky shores. Ecology **85**:1321-1331.

Bierbaum, R. M., and S. Ferson. 1986. Do symbiotic pea crabs decrease growth rate in mussels? The Biological Bulletin **170**:51-61.

Bollen, M., C. N. Battershill, C. A. Pilditch, and K. Bischof. 2017. Desiccation tolerance of different life stages of the invasive marine kelp Undaria pinnatifida: Potential for overland transport as invasion vector. Journal of Experimental Marine Biology and Ecology **496**:1-8.

Borthagaray, A. I., and A. Carranza. 2007. Mussels as ecosystem engineers: their contribution to species richness in a rocky littoral community. Acta Oecologica **31**:243-250.

Buchanan, S., and R. Babcock. 1997. Primary and secondary settlement by the Greenshell mussel *Perna canaliculus*. Journal of Shellfish Research **16**:71-76.

Buschbaum, C., S. Dittmann, J.-S. Hong, I.-S. Hwang, M. Strasser, M. Thiel, N. Valdivia, S.-P. Yoon, and K. Reise. 2009. Mytilid mussels: global habitat engineers in coastal sediments. Helgoland Marine Research **63**:47-58.

Buschbaum, C., and B. Saier. 2001. Growth of the mussel *Mytilus edulis* L. in the Wadden Sea affected by tidal emergence and barnacle epibionts. Journal of Sea Research **45**:27-36.

Camacho, A. P., U. Labarta, and R. Beiras. 1995. Growth of mussels (*Mytilus edulis galloprovincialis*) on cultivation rafts: influence of seed source, cultivation site and phytoplankton availability. Aquaculture **138**:349-362.

Campbell, S. J., J. S. Bite, and T. R. Burridge. 1999. Seasonal patterns in the photosynthetic capacity, tissue pigment and nutrient content of different developmental stages of *Undaria pinnatifida* (phaeophyta: laminariales) in Port Phillip Bay, South-Eastern Australia. Botanica Marina **42**:231-241.

Carr, M. H., J. E. Neigel, J. A. Estes, S. Andelman, R. R. Warner, and J. L. Largier. 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. Ecological Applications:S90-S107.

Casas, G., R. Scrosati, and M. L. Piriz. 2004. The invasive kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). Biological Invasions **6**:411-416.

Castric-Fey, A., A. Girard, and M. T. L'Hardy-Halos. 1993. The distribution of *Undaria pinnatifida* (Phaeophyceae, Laminariales) on the coast of St. Malo (Brittany, France). Botanica Marina **36**:351-358.

Champion, P. D., M. D. de Winton, J. S. Clayton, C. MacNeil, and M. Campbell. 2014. A risk assessment based proactive management strategy for aquatic weeds in New Zealand. Management of Biological Invasions **5**:233-240.

Chandurvelan, R., I. D. Marsden, C. N. Glover, and S. Gaw. 2016. Biomarker responses of mussels exposed to earthquake disturbances. Estuarine, Coastal and Shelf Science **182**:98-111.

Chen, W. W. 2012. Distribution, abundance and reproduction of *Undaria pinnatifida* (Harvey) Suringar from the Marlborough Sounds, New Zealand. MSc Thesis. Auckland University of Technology.

Clarke, K., and R. Gorley. 2006. PRIMER v6: User Manual/tutorial (Plymouth Routines in Multivariate Ecological Research). Plymouth: Primer-E Ltd.

Clavero, M., and E. Garcia-Berthou. 2005. Invasive species are a leading cause of animal extinctions. Trends in Ecology & Evolution **20**:110-110.

Culver, C. S., and A. M. Kuris. 2000. The apparent eradication of a locally established introduced marine pest. Biological Invasions **2**:245-253.

Curiel, D., P. Guidetti, G. Bellemo, M. Scattolin, and M. Marzocchi. 2002. The introduced alga *Undaria pinnatifida* (Laminariales, Alariaceae) in the lagoon of Venice. Hydrobiologia **477**:209-219.

de Sá, F. S., R. C. Nalesso, and K. Paresque. 2007. Fouling organisms on *Perna perna* mussels: is it worth removing them? Brazilian Journal of Oceanography **55**:155-161.

Dean, P. R. 1999. The ecological effects of *Undaria pinnatifida*: A critical assessment and summary of the literature. Conservation Advisory Science Notes **112**:1-34.

Didham, R. K., J. M. Tylianakis, M. A. Hutchison, R. M. Ewers, and N. J. Gemmell. 2005. Are invasive species the drivers of ecological change? Trends in Ecology & Evolution **20**:470-474.

Dittman, D., and C. Robles. 1991. Effect of algal epiphytes on the mussel *Mytilus californianus*. Ecology **72**:286-296.

Enright, C., D. Krailo, L. Staples, M. Smith, C. Vaughan, D. Ward, P. Gaul, and E. Borgese. 1983. Biological control of fouling algae in oyster aquaculture. Journal of Shellfish Research **3**:41-44.

Epstein, G., and D. A. Smale. 2017. *Undaria pinnatifida*: A case study to highlight challenges in marine invasion ecology and management. Ecology and Evolution **7**:8624-8642.

Fletcher, L. M. 2013. Ecology of biofouling and impacts on mussel aquaculture: a case study with *Didemnum vexillum*. PhD Thesis. Victoria University of Wellington.

Forrest, B. M., and K. A. Blakemore. 2006. Evaluation of treatments to reduce the spread of a marine plant pest with aquaculture transfers. Aquaculture **257**:333-345.

Forrest, B. M., and G. A. Hopkins. 2013. Population control to mitigate the spread of marine pests: insights from management of the Asian kelp *Undaria pinnatifida* and colonial ascidian *Didemnum vexillum*. Management of Biological Invasions **4**:317-326.

Forrest, B. M., and M. D. Taylor. 2002. Assessing invasion impact: survey design considerations and implications for management of an invasive marine plant. Biological Invasions **4**:375-386.

Fox, S. P. 2003. The Growth of Cultured *Perna canaliculus* in Pelorus Sound, New Zealand: The Importance of Spat Origin, Environment and Time of Harvest. PhD Thesis. University of Canterbury.

Fréchette, M., and E. Bourget. 1985. Energy flow between the pelagic and benthic zones: factors controlling particulate organic matter available to an intertidal mussel bed. Canadian Journal of Fisheries and Aquatic Sciences **42**:1158-1165.

Galil, B. 2009. Taking stock: inventory of alien species in the Mediterranean Sea. Biological Invasions **11**:359-372.

Gardner, J. P. 2000. Where are the mussels on Cook Strait (New Zealand) shores? Low seston quality as a possible factor limiting multi-species distributions. Marine Ecology Progress Series **194**:123-132.

Gardner, J. P., and R. J. Thompson. 2001. Naturally low seston concentration and the net energy balance of the greenshell mussel (*Perna canaliculus*) at Island Bay, Cook Strait, New Zealand. New Zealand Journal of Marine and Freshwater Research **35**:457-468.

Garen, P., S. Robert, and S. Bougrier. 2004. Comparison of growth of mussel, *Mytilus edulis*, on longline, pole and bottom culture sites in the Pertuis Breton, France. Aquaculture **232**:511-524.

Garner, Y. L., and M. K. Litvaitis. 2017. Effects of artificial epibionts on byssogenesis, attachment strength, and movement in two size classes of the blue mussel, *Mytilus edulis*. Invertebrate Biology **136**:15-21.

Garrabou, J., R. Coma, N. Bensoussan, M. Bally, P. Chevaldonné, M. Cigliano, D. Diaz, J.-G. Harmelin, M. Gambi, and D. Kersting. 2009. Mass mortality in Northwestern Mediterranean rocky benthic communities: effects of the 2003 heat wave. Global Change Biology **15**:1090-1103.

Grosholz, E. D. 2005. Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. Proceedings of the National Academy of Sciences **102**:1088-1091.

Gutiérrez, J. L., C. G. Jones, D. L. Strayer, and O. O. Iribarne. 2003. Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos **101**:79-90.

Hay, C., and E. Villouta. 1993. Seasonality of the adventive Asian kelp *Undaria pinnatifida* in New Zealand. Botanica Marina **36**:461-476.

Hay, C. H. 1990. The dispersal of sporophytes of Undaria pinnatifida by coastal shipping in New Zealand, and implications for further dispersal of *Undaria* in France. British Phycological Journal **25**:301-313.

Hay, C. H., and P. A. Luckens. 1987. The Asian kelp *Undaria pinnatifida* (Phaeophyta: Laminariales) found in a New Zealand harbour. New Zealand Journal of Botany **25**:329-332.

Hewitt, C. L., M. L. Campbell, F. McEnnulty, K. M. Moore, N. B. Murfet, B. Robertson, and B. Schaffelke. 2005. Efficacy of physical removal of a marine pest: the introduced kelp *Undaria pinnatifida* in a Tasmanian Marine Reserve. Biological Invasions **7**:251-263.

Hickman, R. W. 1979. Allometry and growth of the green-lipped mussel *Perna canaliculus* in New Zealand. Marine Biology **51**:311-327.

Hickman, R. W., and J. Illingworth. 1980. Condition cycle of the green-lipped mussel *Perna canaliculus* in New Zealand. Marine Biology **60**:27-38.

Hickman, R. W., R. P. Waite, J. Illingworth, J. L. Meredyth-Young, and G. Payne. 1991. The relationship between farmed mussels, *Perna canaliculus*, and available food in Pelorus-Kenepuru Sound, New Zealand, 1983–1985. Aquaculture **99**:49-68.

Howes, S., C. Herbinger, P. Darnell, and B. Vercaemer. 2007. Spatial and temporal patterns of recruitment of the tunicate *Ciona intestinalis* on a mussel farm in Nova Scotia, Canada. Journal of Experimental Marine Biology and Ecology **342**:85-92.

Hulme, P. E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. Journal of Applied Ecology **46**:10-18.

Hurd, C. L. 2000. Water motion, marine macroalgal physiology, and production. Journal of Phycology **36**:453-472.

Irigoyen, A. J., G. Trobbiani, M. P. Sgarlatta, and M. P. Raffo. 2011. Effects of the alien algae *Undaria pinnatifida* (Phaeophyceae, Laminariales) on the diversity and abundance of benthic macrofauna in Golfo Nuevo (Patagonia, Argentina): potential implications for local food webs. Biological Invasions **13**:1521-1532.

James, K., J. Kibele, and N. T. Shears. 2015. Using satellite-derived sea surface temperature to predict the potential global range and phenology of the invasive kelp *Undaria pinnatifida*. Biological Invasions **17**:3393-3408.

James, K., and N. Shears. 2012. Spatial distribution and seasonal variaton in *Undaria pinnatifida* populations around the Coromandel Peninsula. Technical Report 2013/15. Waikato Regional Council, Hamilton, New Zealand.

James, K., and N. T. Shears. 2016a. Population ecology of the invasive kelp *Undaria pinnatifida* towards the upper extreme of its temperature range. Marine Biology **163**:225.

James, K., and N. T. Shears. 2016b. Proliferation of the invasive kelp *Undaria pinnatifida* at aquaculture sites promotes spread to coastal reefs. Marine Biology **163**:34.

Jernakoff, P. 1983. Factors affecting the recruitment of algae in a midshore region dominated by barnacles. Journal of Experimental Marine Biology and Ecology **67**:17-31.

Johnson, C., J. Valentine, and H. Pederson. 2004. A most unusual barrens: complex interactions between lobsters, sea urchins and algae facilitates spread of an exotic kelp in eastern Tasmania. Pages 213-220 *in* Echinoderms: München: Proceedings of the 11th International Echinoderm Conference, 6-10 October 2003, Munich, Germany. CRC Press.

Katsanevakis, S., I. Wallentinus, A. Zenetos, E. Leppäkoski, M. E. Çinar, B. Oztürk, M. Grabowski, D. Golani, and A. C. Cardoso. 2014. Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. Aquatic Invasions **9**:391-423.

Keller, R. P., J. M. Drake, M. B. Drew, and D. M. Lodge. 2011. Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. Diversity and Distributions **17**:93-102.

Kennedy, V. 1976. Desiccation, higher temperatures and upper intertidal limits of three species of sea mussels (Mollusca: Bivalvia) in New Zealand. Marine Biology **35**:127-137.

Kim, K., T. Choi, S. Huh, and D. Garbary. 1998. Seasonality and community structure of subtidal benthic algae from Daedo Island, southern Korea. Botanica Marina **41**:357-366.

Kluza, D., I. Ridgway, S. Kleeman, and B. Gould. 2006. Organism Impact Assessment: *Styela clava* (Clubbed Tunicate). Biosecurity New Zealand, Wellington, New Zealand.

Lachowicz, Ł. S. 2005. Population biology of mussels (*Aulacomya maoriana*, *Mytilus galloprovincialis* and *Perna canaliculus*) from rocky intertidal shores in Wellington Harbour, New Zealand. PhD Thesis. Victoria University of Wellington, New Zealand.

Laihonen, P., and E. Furman. 1986. The site of settlement indicates commensalism between blue mussel and its epibiont. Oecologia **71**:38-40.

Lander, T. R., S. M. Robinson, B. A. MacDonald, and J. D. Martin. 2012. Enhanced growth rates and condition index of blue mussels (*Mytilus edulis*) held at integrated multitrophic aquaculture sites in the Bay of Fundy. Journal of Shellfish Research **31**:997-1007.

Laudien, J., and M. Wahl. 1999. Indirect effects of epibiosis on host mortality: seastar predation on differently fouled mussels. Marine Ecology **20**:35-47.

Lemieux, J., and M. Cusson. 2014. Effects of habitat-forming species richness, evenness, identity, and abundance on benthic intertidal community establishment and productivity. PloS ONE **9**:e109261.

Lilley, S. A., T. Alestra, M. Hickford, and D. R. Schiel. 2016. Biodiversity and community composition of rocky intertidal areas within Whakaraupō/Lyttelton Harbour.

Lourey, M. J., D. A. Ryan, and I. R. Miller. 2000. Rates of decline and recovery of coral cover on reefs impacted by, recovering from and unaffected by crown-of-thorns starfish *Acanthaster planci*: a regional perspective of the Great Barrier Reef. Marine Ecology Progress Series **196**:179-186.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the world's worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group, Auckland, New Zealand.

Luckens, P. A. 1975. Predation and intertidal zonation of barnacles at Leigh, New Zealand. New Zealand Journal of Marine and Freshwater Research **9**:355-378.

MAF. 2010. The commercial use of *Undaria pinnatifida* - an exotic Asian seaweed. Information Paper No: 2010/02. MAF Biosecurity New Zealand. Ministry of Agriculture and Forestry. Wellington, New Zealand.

Maggi, E., L. Benedetti-Cecchi, A. Castelli, E. Chatzinikolaou, T. Crowe, G. Ghedini, J. Kotta, D. Lyons, C. Ravaglioli, and G. Rilov. 2015. Ecological impacts of invading seaweeds: a meta-analysis of their effects at different trophic levels. Diversity and Distributions **21**:1-12.

Marsden, I. D., and M. A. Weatherhead. 1999. Shore-level induced variations in condition and feeding of the mussel *Perna canaliculus* from the east coast of the South Island, New Zealand. New Zealand Journal of Marine and Freshwater Research **33**:611-622.

Medcof, J., and A. Needler. 1941. The influence of temperature and salinity on the condition of oysters (*Ostrea virginica*). Journal of the Fisheries Board of Canada **5**:253-257.

Migné, A., C. Golléty, and D. Davoult. 2015. Effect of canopy removal on a rocky shore community metabolism and structure. Marine Biology **162**:449-457.

Molnar, J. L., R. L. Gamboa, C. Revenga, and M. D. Spalding. 2008. Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment **6**:485-492.

Morita, T., A. Kurashima, and M. Maegawa. 2003. Temperature requirements for the growth and maturation of the gametophytes of *Undaria pinnatifida* and *U. undarioides* (Laminariales, Phaeophyceae). Phycological Research **51**:154-160.

Nanba, N., T. Fujiwara, K. Kuwano, Y. Ishikawa, H. Ogawa, and R. Kado. 2011. Effect of water flow velocity on growth and morphology of cultured *Undaria pinnatifida* sporophytes (Laminariales, Phaeophyceae) in Okirai Bay on the Sanriku coast, Northeast Japan. Journal of Applied Phycology **23**:1023-1030.

NIWA. 2018. New Zealand Climate Update, January 2018. NIWA, Wellington, New Zealand.

O'Connor, N. E. 2010. Shore exposure affects mussel population structure and mediates the effect of epibiotic algae on mussel survival in SW Ireland. Estuarine, Coastal and Shelf Science **87**:83-91.

O'Connor, N. E., T. P. Crowe, and D. McGrath. 2006. Effects of epibiotic algae on the survival, biomass and recruitment of mussels, *Mytilus* L. (Bivalvia: Mollusca). Journal of Experimental Marine Biology and Ecology **328**:265-276.

Occhipinti-Ambrogi, A. 2007. Global change and marine communities: alien species and climate change. Marine Pollution Bulletin **55**:342-352.

Okumuş, İ., and H. P. Stirling. 1998. Seasonal variations in the meat weight, condition index and biochemical composition of mussels (*Mytilus edulis* L.) in suspended culture in two Scottish sea lochs. Aquaculture **159**:249-261.

Oliver, E. C., J. A. Benthuysen, N. L. Bindoff, A. J. Hobday, N. J. Holbrook, C. N. Mundy, and S. E. Perkins-Kirkpatrick. 2017. The unprecedented 2015/16 Tasman Sea marine heatwave. Nature Communications **8**:16101.

Orban, E., G. Di Lena, T. Nevigato, I. Casini, A. Marzetti, and R. Caproni. 2002. Seasonal changes in meat content, condition index and chemical composition of mussels (*Mytilus galloprovincialis*) cultured in two different Italian sites. Food Chemistry **77**:57-65.

Ormsby, M., and E. Brenton-Rule. 2017. A review of global instruments to combat invasive alien species in forestry. Biological Invasions **19**:3355-3364.

Paine, R. T. 1979. Disaster, catastrophe, and local persistence of the sea palm *Postelsia palmaeformis*. Science **205**:685-687.

Parker, I. M., D. Simberloff, W. Lonsdale, K. Goodell, M. Wonham, P. Kareiva, M. Williamson, B. Von Holle, P. Moyle, and J. Byers. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions **1**:3-19.

Peharda, M., I. Župan, L. Bavčević, A. Frankić, and T. Klanjšček. 2007. Growth and condition index of mussel *Mytilus galloprovincialis* in experimental integrated aquaculture. Aquaculture Research **38**:1714-1720.

Pereyra, P. J., M. Arias, R. A. C. González, and M. A. Narvarte. 2014. Moving forward: the Japanese kelp *Undaria pinnatifida* (Harvey) Suringar, 1873 expands in northern Patagonia, Argentina. BioInvasions Records **3**:65-70.

Pereyra, P. J., P. de la Barra, M. Gastaldi, J. F. Saad, F. N. Firstater, and M. A. Narvarte. 2017. When the tiny help the mighty: facilitation between two introduced species, a solitary ascidian and a macroalga in northern Patagonia, Argentina. Marine Biology **164**:185.

Perez, R., R. Kaas, and O. Barbaroux. 1984. Culture expérimentale de l'algue *Undaria pinnatifida* sur les côtes de France. Science et peche **343**:3-16.

Peteiro, C., and Ó. Freire. 2011. Effect of water motion on the cultivation of the commercial seaweed *Undaria pinnatifida* in a coastal bay of Galicia, Northwest Spain. Aquaculture **314**:269-276.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics **52**:273-288.

Powell, A. W. B. 1979. New Zealand Mollusca: marine, land, and freshwater shells. Collins.

RCoreTeam. 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria.

Riera, P., L. Stal, and J. Nieuwenhuize. 2002. δ13C versus δ15N of co-occurring molluscs within a community dominated by *Crassostrea gigas* and *Crepidula fornicata* (Oosterschelde, The Netherlands). Marine Ecology Progress Series **240**:291-295.

Ross, D., C. Johnson, C. Hewitt, and G. M. Ruiz. 2004. Interaction and impacts of two introduced species on a soft-sediment marine assemblage in SE Tasmania. Marine Biology **144**:747-756.

RStudioTeam. 2016. RStudio: Integrated Development Environment for R. RStudio, Inc.

Russell, L. K., C. D. Hepburn, C. L. Hurd, and M. D. Stuart. 2008. The expanding range of *Undaria pinnatifida* in southern New Zealand: distribution, dispersal mechanisms and the invasion of wave-exposed environments. Biological Invasions **10**:103-115.

Saito, Y. 1975. Practical significance of algae in Japan. *Undaria*. Advance of Phycology in Japan:304-320.

Santelices, B., and E. Martinez. 1988. Effects of filter-feeders and grazers on algal settlement and growth in mussel beds. Journal of Experimental Marine Biology and Ecology **118**:281-306.

Schaffelke, B., M. L. Campbell, and C. L. Hewitt. 2005. Reproductive phenology of the introduced kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) in Tasmania, Australia. Phycologia **44**:84-94.

Schaffelke, B., and C. L. Hewitt. 2007. Impacts of introduced seaweeds. Botanica Marina **50**:397-417.

Schaffelke, B., J. E. Smith, and C. L. Hewitt. 2006. Introduced macroalgae - a growing concern. Journal of Applied Phycology **18**:529-541.

Schiel, D. R., S. A. Lilley, and P. M. South. 2018. Ecological tipping points for an invasive kelp in rocky reef algal communities. Marine Ecology Progress Series **587**:93-104.

Schiel, D. R., and G. A. Thompson. 2012. Demography and population biology of the invasive kelp *Undaria pinnatifida* on shallow reefs in southern New Zealand. Journal of Experimental Marine Biology and Ecology **434**:25-33.

Schmidt, A. L., and R. E. Scheibling. 2006. A comparison of epifauna and epiphytes on native kelps (*Laminaria* species) and an invasive alga (*Codium fragile* ssp. *tomentosoides*) in Nova Scotia, Canada. Botanica Marina **49**:315-330.

Sellheim, K., J. J. Stachowicz, and R. C. Coates. 2010. Effects of a nonnative habitat-forming species on mobile and sessile epifaunal communities. Marine Ecology Progress Series **398**:69-80.

Shepherd, S., and G. Edgar. 2013. Ecology of Australian temperate reefs: the unique South. CSIRO Publishing, Collingwood, VIC, Australia.

Silliman, B. R., M. D. Bertness, A. H. Altieri, J. N. Griffin, M. C. Bazterrica, F. J. Hidalgo, C. M. Crain, and M. V. Reyna. 2011. Whole-community facilitation regulates biodiversity on Patagonian rocky shores. PloS ONE **6**:e24502.

Silva, P. C., R. A. Woodfield, A. N. Cohen, L. H. Harris, and J. H. Goddard. 2002. First report of the Asian kelp *Undaria pinnatifida* in the northeastern Pacific Ocean. Biological Invasions **4**:333-338.

Simberloff, D. 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? Ecology Letters **9**:912-919.

Sinner, J., B. Forrest, and M. Taylor. 2000. A strategy for managing the Asian kelp *Undaria*: final report. Cawthron Institute, Nelson, New Zealand.

Sliwa, C., C. R. Johnson, and C. L. Hewitt. 2006. Mesoscale dispersal of the introduced kelp *Undaria pinnatifida* attached to unstable substrata. Botanica Marina **49**:396-405.

South, P., S. Lilley, L. Tait, T. Alestra, M. Hickford, M. Thomsen, and D. Schiel. 2016. Transient effects of an invasive kelp on the community structure and primary productivity of an intertidal assemblage. Marine and Freshwater Research **67**:103-112.

South, P. M., O. Floerl, B. M. Forrest, and M. S. Thomsen. 2017. A review of three decades of research on the invasive kelp *Undaria pinnatifida* in Australasia: An assessment of its success, impacts and status as one of the world's worst invaders. Marine Environmental Research **131**:243-257.

South, P. M., and M. S. Thomsen. 2016. The ecological role of invading *Undaria pinnatifida*: an experimental test of the driver–passenger models. Marine Biology **163**:175.

Stachowicz, J. J., J. R. Terwin, R. B. Whitlatch, and R. W. Osman. 2002. Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. Proceedings of the National Academy of Sciences **99**:15497-15500.

Suárez Jiménez, R. 2015. The ecology of the invasive kelp *Undaria pinnatifida*: functioning at an ecosystem level. PhD Thesis. University of Otago, Dunedin, New Zealand.

Suárez Jiménez, R., C. D. Hepburn, G. A. Hyndes, R. J. McLeod, R. B. Taylor, and C. L. Hurd. 2015. Do native subtidal grazers eat the invasive kelp *Undaria pinnatifida*? Marine Biology **162**:0. https://doi.org/10.1007/s00227-00015-02757-y.

Tait, L. W., P. M. South, S. A. Lilley, M. S. Thomsen, and D. R. Schiel. 2015. Assemblage and understory carbon production of native and invasive canopy-forming macroalgae. Journal of Experimental Marine Biology and Ecology **469**:10-17.

Teso, S. V., G. Bigatti, G. N. Casas, M. L. Piriz, and P. E. Penchaszadeh. 2009. Do native grazers from Patagonia, Argentina consume the invasive kelp *Undaria pinnatifida*. Revista del Museo Argentino de Ciencias Naturales **11**:7-14.

Thiel, M., and J. A. Vásquez. 2000. Are kelp holdfasts islands on the ocean floor?—Indication for temporarily closed aggregations of peracarid crustaceans. Pages 45-54 *in* M. B. Jones, J. M. N. Azevedo, A. I. Neto, A. C. Costa, and A. M. F. Martins, editors. Island, Ocean and Deep-Sea Biology. Springer, Dordrecht.

Thieltges, D. W. 2005. Impact of an invader: epizootic American slipper limpet *Crepidula fornicata* reduces survival and growth in European mussels. Marine Ecology Progress Series **286**:13-19.

Thieltges, D. W., and C. Buschbaum. 2007. Mechanism of an epibiont burden: *Crepidula fornicata* increases byssus thread production by *Mytilus edulis*. Journal of Molluscan Studies **73**:75-77.

Thompson, G. A. 2004. Mechanisms of invasion and persistence of the invasive kelp *Undaria pinnatifida* (Harvey) Suringar within intertidal areas of southern New Zealand. PhD Thesis. University of Canterbury, Christchurch, New Zealand.

Thompson, G. A., and D. R. Schiel. 2012. Resistance and facilitation by native algal communities in the invasion success of *Undaria pinnatifida*. Marine Ecology Progress Series **468**:95-105.

Thomsen, M. S., L. Mondardini, T. Alestra, S. Gerrity, and D. R. Schiel 2018. The Tasman Sea 2017/18 Marine Heatwave Annihilated Bull Kelp around Christchurch. Poster presented at The Pop Up Christchurch Climate Ex-change 28/3-2018, Christchurch, New Zealand.

Thomsen, M. S., J. D. Olden, T. Wernberg, J. N. Griffin, and B. R. Silliman. 2011. A broad framework to organize and compare ecological invasion impacts. Environmental Research **111**:899-908.

Thomsen, M. S., P. A. Stæhr, L. Nejrup, and D. R. Schiel. 2013. Effects of the invasive macroalgae *Gracilaria vermiculophylla* on two co-occurring foundation species and associated invertebrates. Aquatic Invasions **8**:133–145.

Thomsen, M. S., T. Wernberg, A. Altieri, F. Tuya, D. Gulbransen, K. J. McGlathery, M. Holmer, and B. R. Silliman. 2010. Habitat cascades: the conceptual context and global relevance of facilitation cascades via habitat formation and modification. Integrative and Comparative Biology **50**:158-175.

Thomsen, M. S., T. Wernberg, P. M. South, and D. R. Schiel. 2016a. Non-native seaweeds drive changes in marine coastal communities around the world. Pages 147-185 *in* Z.-M. Hu and C. Fraser, editors. Seaweed Phylogeography. Springer, Dordrecht.

Thomsen, M. S., T. Wernberg, P. M. South, and D. R. Schiel. 2016b. To include or not to include (the invader in community analyses)? That is the question. Biological Invasions **18**:1515-1521.

Thomsen, M. S., T. Wernberg, F. Tuya, and B. R. Silliman. 2009. Evidence for impacts of nonindigenous macroalgae: A meta-analysis of experimental field studies. Journal of Phycology **45**:812-819.

Thornber, C., B. Kinlan, M. Graham, and J. Stachowicz. 2004. Population ecology of the invasive kelp *Undaria pinnatifida* in California: Environmental and biological controls on demography. Marine Ecology Progress Series **268**:69-80.

Tsuchiya, M. 1983. Mass mortality in a population of the mussel *Mytilus edulis* L. caused by high temperature on rocky shores. Journal of Experimental Marine Biology and Ecology **66**:101-111.

Tuya, F., K. Larsen, and V. Platt. 2011. Patterns of abundance and assemblage structure of epifauna inhabiting two morphologically different kelp holdfasts. Hydrobiologia **658**:373-382.

Underwood, A. 1980. The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. Oecologia **46**:201-213.

Valdivia, N., and M. Thiel. 2006. Effects of point-source nutrient addition and mussel removal on epibiotic assemblages in *Perumytilus purpuratus* beds. Journal of Sea Research **56**:271-283.

Valentine, J. P., and C. R. Johnson. 2003. Establishment of the introduced kelp *Undaria pinnatifida* in Tasmania depends on disturbance to native algal assemblages. Journal of Experimental Marine Biology and Ecology **295**:63-90.

Valentine, J. P., and C. R. Johnson. 2005. Persistence of the exotic kelp *Undaria pinnatifida* does not depend on sea urchin grazing. Marine Ecology Progress Series **285**:43-55.

Vinther, H. F., and M. Holmer. 2008. Experimental test of biodeposition and ammonium excretion from blue mussels (*Mytilus edulis*) on eelgrass (*Zostera marina*) performance. Journal of Experimental Marine Biology and Ecology **364**:72-79.

Wahl, M. 1989. Marine epibiosis. I. Fouling and antifouling: some basic aspects. Marine Ecology Progress Series **58**:175-189.

Wernberg, T., S. Bennett, R. C. Babcock, T. de Bettignies, K. Cure, M. Depczynski, F. Dufois, J. Fromont, C. J. Fulton, and R. K. Hovey. 2016. Climate-driven regime shift of a temperate marine ecosystem. Science **353**:169-172.

Williams, J. A., and C. J. West. 2000. Environmental weeds in Australia and New Zealand: issues and approaches to management. Austral Ecology **25**:425-444.

Williams, S. L., and J. E. Smith. 2007. A global review of the distribution, taxonomy, and impacts of introduced seaweeds. Annual Review of Ecology, Evolution, and Systematics **38**:327-359.

Woods, C. M. C., O. Floerl, and B. J. Hayden. 2012. Biofouling on Greenshell (TM) mussel (*Perna canaliculus*) farms: a preliminary assessment and potential implications for sustainable aquaculture practices. Aquaculture International **20**:537-557.

Wotton, D. M., C. O'Brien, M. D. Stuart, and D. J. Fergus. 2004. Eradication success down under: heat treatment of a sunken trawler to kill the invasive seaweed *Undaria pinnatifida*. Marine Pollution Bulletin **49**:844-849.

Zardi, G., K. Nicastro, C. McQuaid, T. Ng, J. Lathlean, and L. Seuront. 2016. Enemies with benefits: parasitic endoliths protect mussels against heat stress. Scientific Reports **6**:31413.